



Det här verket har digitaliserats vid Göteborgs universitetsbibliotek och är fritt att använda. Alla tryckta texter är OCR-tolkade till maskinläsbar text. Det betyder att du kan söka och kopiera texten från dokumentet. Vissa äldre dokument med dåligt tryck kan vara svåra att OCR-tolka korrekt vilket medför att den OCR-tolkade texten kan innehålla fel och därför bör man visuellt jämföra med verkets bilder för att avgöra vad som är riktigt.

This work has been digitized at Gothenburg University Library and is free to use. All printed texts have been OCR-processed and converted to machine readable text. This means that you can search and copy text from the document. Some early printed books are hard to OCR-process correctly and the text may contain errors, so one should always visually compare it with the images to determine what is correct.



Nils Rosen

INSTITUTE OF FRESHWATER RESEARCH, DROTTHINGHOLM

REPORT No 33

FISHERY BOARD OF SWEDEN

ANNUAL REPORT

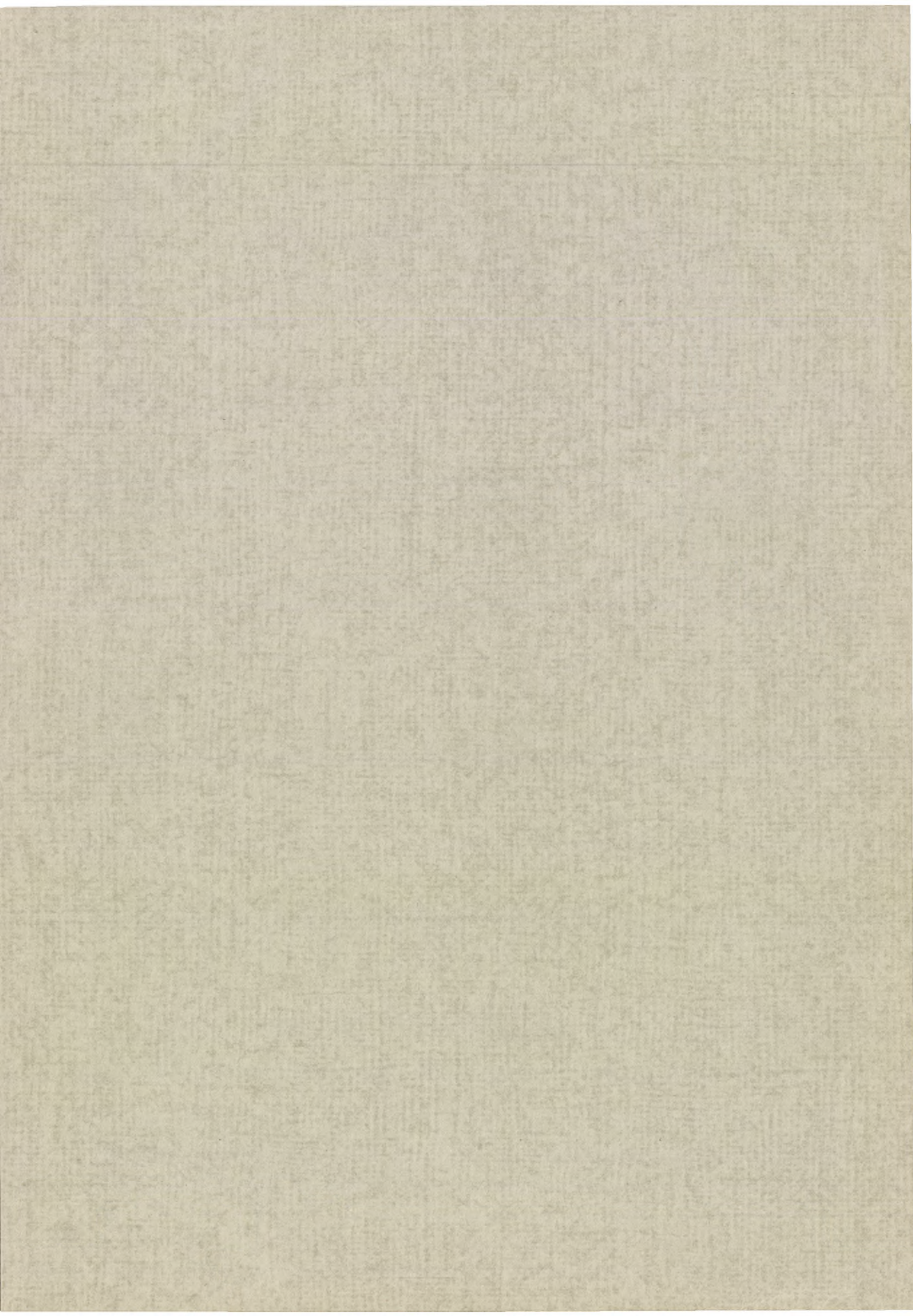
FOR THE YEAR 1951

AND

SHORT PAPERS

LUND 1952

CARL BLOMS BOKTRYCKERI A.-B.



INSTITUTE OF FRESHWATER RESEARCH, DROTTHINGHOLM

REPORT No 33

FISHERY BOARD OF SWEDEN

ANNUAL REPORT

FOR THE YEAR 1951

AND

SHORT PAPERS

LUND 1952

CARL BLOMS BOKTRYCKERI A.-B.

Table of Contents

Director's report for the year 1951; <i>Sven Runnström</i>	5
<i>Short papers:</i>	
Year Class Fluctuations and Span of Life of Perch; <i>Gunnar Alm</i>	17
Zur Kenntnis der Taxonomie und Metamorphose der Chironomidengattungen <i>Protanypus</i> KIEFF., <i>Prodiamesa</i> KIEFF. und <i>Monodiamesa</i> KIEFF.; <i>Lars Brundin</i>	39
Accessories for the determination of dissolved oxygen; <i>Leif Bruneau</i>	54
Salmon Tagging Experiments in Sundsvall Bay of the Baltic in 1950; <i>Arne Lindroth</i>	57
Sur l'écologie du zooplancton Crustacé; <i>Thorolf Lindström</i>	70
Beitrag zur Fauna einiger Wasseransammlungen in der Balsberggrotte; <i>Heinz Löffler</i>	166
Pike-perch studies in Lake Vänern; <i>Carl Puke</i>	168
The Population of Trout, <i>Salmo trutta</i> , LINNÉ, in Regulated Lakes; <i>Sven Runnström</i>	179
Spawning Behaviour of <i>Leuciscus rutilus</i> (LINNÉ); <i>Gunnar Svärdson</i>	199
The Coregonid Problem. IV. The Significance of Scales and Gillrakers; <i>Gunnar Svärdson</i>	204

Director's Report for the Year 1951

By SVEN RUNNSTRÖM

Members of the Staff in January 1952

Director:	SVEN RUNNSTRÖM, fil. dr.
Fishery Biologists:	LARS BRUNDIN, fil. dr. GUNNAR SVÄRDSON, fil. dr. THOROLF LINDSTRÖM, fil. dr. ERIC FABRICIUS, fil. dr. KARL-JAKOB GUSTAFSON, fil. kand. MAJ STUBE, fil. kand.
Secretary:	STIG PERSSON, pol. mag.
Fishery Assistants:	GÖSTA MOLIN HENDRIK TOOTS ARNE JOHANSON BIRGER AHLMÉR EGON AHL
Assistant Secretaries:	BIRGIT ERICSSON RUT LARSSON
Laboratory Assistants:	INGRID JOHANNISSON HELVE TOOTS
Porter:	HENNING JOHANSON
Kälarne Research Station (in the province of Jämtland)	
Fishery Assistant:	ELOF HALVARSSON

NILS O. ÖSTERBERG has served as extra laboratory assistant. The Chairman of the Migratory Committee: fil. dr. GUNNAR ALM and three members of the staff, Assistant: dr. VOLDEMAR MIEZIS, Fishery Assistant KARL-BÅDO JOHANSON and Laboratory Assistant: ANNA HÄGGLUND had their office at the Institute last year.

Scientific and Practical Work by the Staff

Studies of the Bottom and Plankton Fauna

BRUNDIN has continued his investigations of the bottom fauna with special regard to the chironomids as indicators in different types of lakes. The material collected confirms the significance of the chironomids in this respect and gives additional verification of the close connection between on the one hand temperature, oxygen pressure and food supplies, on the other the composition of the bottom fauna. In the oligotrophic lakes of the south and middle of Sweden, which are stable in stratification and poor in humus, the profundal bottoms consequently seem to be almost throughout populated by a typical »*Tanytarsus*-fauna» with cold-stenothermal polyoxybiontic species dominating, most of them being chironomids.

Previous investigations have shown that larvae of the genus *Microspectra* play an important role in the deep fauna of the North European *Tanytarsus*-lakes. It has not been possible, however, to make a closer identification. The present material shows that the species in question is *Microspectra insignilobus* KIEFF., previously only known from mountain lakes in the Jotunheim District in Norway. This species is thus a typical member of the *Tanytarsus*-fauna, and all Swedish representatives for this interesting ecological group are now probably identified.

BRUNDIN has previously established that the profundal bottoms in the Scandinavian mountain lakes and in the deepest lakes in the south and middle of Sweden are characterized by a »*Heterotrissocladus*-fauna», an indicator of an environment extremely deficient in food and very rich in oxygen. It is apparent on the bottom samples from the approximately 120 m. deep Lake Siljan in Dalarna, that the lower profundal area in this lake as well is populated by the *Heterotrissocladus*-fauna very deficient both in species and individuals, a not unexpected parallel to the conditions in Lake Vättern.

The bottom fauna in the high arctic lakes of Scandinavia has hitherto been unknown. Material from high arctic lakes (1,450—1,840 m. above sea level) collected in Dovre and Jotunheim in central Norway by K. THOMASSON, Uppsala, and studied by BRUNDIN has made the first contribution to knowledge in the matter. Characteristic for these lakes are first and foremost *Pseudodiamesa nivosa* GOETGH. and *Oeklandia borealis* KIEFF., the latter hitherto only known from Novaya Zemlya.

In co-operation with Professor THIENEMANN, Plön, BRUNDIN has done the preliminary work for a monograph on the *Tanytarsus*-group, which is also of importance from a fishery-biological point of view. Classification tables of larvae, pupae and imagines can probably be printed during the course of the coming year. BRUNDIN has also concluded a revision of imagines and immature forms of the chironomid genera *Protanytus*, *Prodiamesa* and

Monodiamesa, which have played an important part for a long while as indicators of limnic environments. The North Fennoscandian and Alpine lakes are inhabited by separate *Protanypus*- and *Monodiamesa*-species, which form typical boreoalpine pairs of species.

During the year STUBE has completed her field collections in L. Borgasjön regarding the epifauna on various water plants and the identification of the different forms is practically finished.

Examination of stomach samples from trout has shown that the epifauna is of great importance as nourishment for the young fish of this species. During the summer of 1951 STUBE has also commenced investigations of the vegetation areas and bottom fauna in Russfjärden in the River Faxälven (Jämtland). This lake is going to be lowered approximately 1 metre through regulation in the winter and it is, therefore, of considerable interest to determine in what way such a lowering of the water level influences the production within the littoral area.

The quantitative plankton investigations carried out by LINDSTRÖM during the years 1945—1951 are described in a paper in this Report. The investigations have been primarily aimed at studying the supply of plankton in its capacity as potential fish food. This demands a correct method of sampling and a correct statistical analysis of the values obtained — two domains where no generally accepted norms within plankton research are as yet to be found. Actually this lack of norms has led to the entire primary material being included in the article.

A correct estimation of plankton abundance cannot be made without a knowledge of the annual rhythm, distribution and migrations of the plankton because if, for example, marked zones of concentration were not subjected to sampling, no exact picture of the plankton abundance could be obtained. A primary condition for a study of plankton abundance is clearly some knowledge of the ecology of the plankton in the lakes concerned and it is, consequently, plankton ecology which is dealt with in the present paper.

There can be no question of an exhaustive analysis of causality. The sensitivity to light of the plankton is a question which has previously been studied in very great detail as has the plankton populations' dependence on or independence of the changes in season. The annual rhythm of the copepods is, however, not as well known as that of the *Cladocera*, for which reason the former is the subject of a more detailed discussion. New working hypotheses to explain the distribution of the plankton must be drawn up with the greatest caution. As hypotheses have been given the influence of the wind on the distribution of the plankton and the significance of viscosity for the diurnal migrations of the *Cladocera*.

Apart from these questions dissimilarities between lakes and different localities in the same lake (littoral, pelagial, proximity to inflow or outflow) are dealt with, without a more detailed discussion of the causality.

The results obtained render possible an estimate of abundance from the primary material now collected. In particular the stirring-up effect of the wind and the difference between vertical distribution by day and night provide good starting-points for an estimation of this sort. The working out of such an estimation must, however, be left to the future.

Testing the Effectiveness of Artificial Propagation.

Pike: SVÄRDSON's investigations have continued during 1951 according to an unchanged program. In the spring of 1951 spawning fishing began at Drottningholm on April 17th and in L. Halmsjön on April 22nd. The spawning fishing resulted in 243 pike being caught at Drottningholm and 87 pike in L. Halmsjön. After the spawning and up to the commencement of the spawning in 1952 only 29 were caught at Drottningholm, mainly depending on lack of time, and in L. Halmsjön 213 fish. The proportion of pike caught during spawning fishing as compared with the other fishing during the catch year is, for the third year in succession, very different at Drottningholm and in L. Halmsjön. The probable reason is that the pike has comparatively poor spawning-grounds in L. Halmsjön, so that it is difficult there to catch as great a part of the population during spawning as at Drottningholm.

Locality	Beginning of catch year	Number of pike caught:		Totals	
		spawning fishing	other fishing		
Drottningholm ..	1945—46	March 27	255	45	300
	1946—47	April 4	343	80	423
	1947—48	» 18	223	82	305
	1948—49	» 3	190	25	215
	1949—50	» 8	163	43	206
	1950—51	March 30	252	19	271
	1951—52	April 17	243	29	272
Halmsjön	1949—50	April 6	80	292	372
	1950—51	» 4	126	110	236
	1951—52	» 22	87	213	300

The difference between the shore area at Drottningholm and Halmsjön is interesting as it shows that the apprehensions that spawning fishing is over-fishing are exaggerated — quite apart from whether they are right in principle or not — in addition one must take into consideration a strong local variation depending on the shore conditions of the lake. In both areas fishing is carried on as intensively as circumstances permit.

15 of the 274 fin-cut fingerlings planted at Drottningholm in the summer of 1947 had been recaptured up to and including the last report, to which must be added a further 7 specimens captured during the catch year 1951—

1952. Only 3 new specimens of the 699 fingerlings planted in 1948 were recaptured during the new catch year, in addition to the 8 previously recaptured. It seems, accordingly, that very different results are obtained in different years from the planting of fingerlings. It will be of great interest to study this variation closer. New plantings were commenced at Drottningholm in 1951, after their having been confined to L. Halmsjön in the years 1949 and 1950, where no recoveries at all have, however, as yet been made.

In the regional pike investigation, where catch statistics are collected from 15 different fishermen and plantings of newly-hatched fry are made every other year, reports were received during 1951 from all the fishermen with altogether 5,437 scale samples. In all 28,840 scale samples accompanied by particulars as to length, weight and date of catch, tackle and sex have been collected during this investigation. This constitutes an unexampled material for judging the average size of the pike, which are caught during normal fishing in Swedish lakes.

The colour mutants mentioned in previous annual reports have at last during 1951 given rise to a new generation. A total of 19 one-summer-old fingerlings were collected from the ponds in the autumn of 1951. They were just like their parents and definite proof has, thus, been gained that the variation in colour was genetically based. The last parent fish died during the year.

Char: ALM has continued the collecting of fishery statistics and scale samples from Lake Vättern with a view to establishing the strength of the various year classes during periods of planting of fry and periods of natural spawning only. In 1944 the planting of fry ceased, and the year class originating from 1942—43 has, consequently, been the last hatchery supported one. It has, in all probability, not been part of the catches later than the year 1950, so that the catch in 1951 has entirely consisted of naturally-hatched year classes. This year 54,000 kg was obtained as compared to an average of 59,000 kg for the years 1945—49. An analysis of the size of the char caught during the years 1946—51 at one of the chief fishing-grounds compared with the corresponding figures for the years 1924—1933 (ALM, G., 1934 Rept Inst. Freshwater Res. Drottningholm, 2: 1—26) has shown that they have been similar in character during these years.

The recruitment of smaller char from new year classes has not diminished during the last few years, which ought to have been the case, if the hatchery fry had had any particular influence on the abundance of the year classes and this addition gradually came to an end. Admittedly during the years 1924—33 a great deal of small char were caught, but this is connected with no minimum size existing at that time. This minimum size, 36 cm, was first introduced in the year 1938. The number of char of the length group 36—40 cm caught during later years corresponds to the total of the number of char previously captured belonging to all the length groups up to 40 cm.

Char in Lake Vättern: frequency of different length groups.

Year	26—30	31—35	36—40	41—45	46—50	51—55	56—60	61—65	66—70	71—76	Total
1924—	23	110	134	281	149	66	27	15	1	—	806
1933	2.8	13.6	16.6	34.9	18.5	8.2	3.3	1.9	0.1	—	100.0
1946—	—	43	1832	2104	1360	724	282	107	49	9	6511
1951	—	0.7	28.1	32.3	20.9	11.1	4.3	1.6	0.7	0.1	100.0
1950	—	23	496	639	450	233	100	24	8	1	1974
		1.2	25.1	32.4	22.8	11.8	5.1	1.2	0.4	0.05	100.0
1951	—	5	343	363	308	194	78	27	10	1	1329
		0.4	25.8	27.3	23.2	14.6	5.9	2.0	0.7	0.1	100.0

Trout. 10,500 fin-cut fingerlings were planted each year during the years 1948 and 1949 in Lake Storsjouten (Jämtland), in order to test the effectiveness of planting one-summer-old trout fingerlings. The fingerlings were planted in the lower part of feeder streams and consisted in the year 1948 of Swedish trout, while the fingerlings planted in the year 1949 came from roe imported from Denmark. Test fishing with nets has been carried out by AHLMÉR during the years 1950—1952, a total of 1394 trout being caught in the lake. 39 of these were fingerlings fin-cut in 1948 and 4 were the Danish trout marked in 1949. The planted fingerlings have, consequently, only made a very slight contribution as yet to the population. Test fishing will be continued during the coming years.

Control of Fish Populations

Salmon. By continued compilation of age-analyses and statistical material from the salmon catches in the Baltic and its most important salmon rivers, ALM has established that the last year classes are not as rich as the year classes during most years in the forties. Statistical data from the net-fishing in the southern Baltic too has shown that, by using an equal quantity of gear, the catches of salmon in the year 1951 only amounted to about half the number of salmon caught in the year 1950. Yet the age distribution in the catches is, roughly speaking, normal with the five- and six-year-old salmon predominating, the catches of small salmon under 3 kg being of about the same size as during the last few years.

Trout. GUSTAFSON's investigations concerning the trout population of Lake Storsjön were continued during the year 1951, partly at a fish ladder in the Dammån, partly at two weirs, one in the Dammån between the mouth and the fish ladder, the other at the mouth of the Storboströmmen in Lake Ockesjön. The control at the fish ladder lasted from the 17.6—15.10, 662 trout being marked. 154 trout were caught and marked at the weir in the Dammån, 53 of which were recaptured in the ladder situated upstream. A roe sample

placed on a spawning-ground showed that hatching occurred about the 1st of May. In the Storboströmmen migration upstream for spawning began during the first days in August, but on account of unfavourable log-floating conditions the weir could first be erected during the period 13.9—5.12, so that only 13 trout were captured going upstream.

RUNNSTRÖM's studies of the migrations of the trout in the fish ladder at Lake Rensjön in 1951 show a migration upstream from the outflowing river to the lake of 447 young fish during the period 3.6—14.10. During June and July 15 large trout, that had spawned the previous autumn, also migrated upstream. Migration downstream of spawning fish during August and September was inconsiderable this year and comprised only 3 ♂♂ and 5 ♀♀.

Char. The spawning migration of the char in the stream Blåsjöälven was controlled this year as well by the erection of a weir. During their migration upstream 5,664 fish were obtained but on their way downstream not less than 15,120 fish, which shows that the weir was not effective for the char going upstream. 1,450 of these fish were marked.

Grayling. From GUSTAFSON's investigations of the spawning migration upstream in the Svartbäcken (Storsjön, Jämtland) in the spring of 1951, it appeared that the population consists of 202 fish, 55 of which were marked during the control the previous year. In three other spawning streams as well, resp. 2, 5 and 10 km from the Svartbäcken, there were recoveries of grayling previously marked in the Svartbäcken. Thus, for example, 4 fish were marked of the 22 caught in the Hegledbäcken, 2 were marked out of 180 captured in the Örnvedebäcken and 1 was marked out of 347 caught in the Harån.

During the period July—November 792 one-summer-old fish and 4 several-summers-old fish migrated down the Svartbäcken.

Whitefish. TOOTS' investigations at the so-called »Vaktfisket» in the Gimån have been continued in order to follow the variations in strength of the year classes and the growth of the fish.

A. JOHANSON also continued the control of the stunted whitefish population in the Nästån in Jämtland with an improved weir, 8,000 kg of whitefish being caught to reduce the population. Scale samples were taken of 563 fish and the number of gillrakers was counted in 375 fish. Study of this material seems to indicate that the whitefish, which first makes its way to the spawning-stream, is a different species (22—23 gillrakers) from those appearing later in the season (33—34 gillrakers).

Studies on the Spawning Behaviour of Fish

Char. In the autumn of 1951 FABRICIUS studied the spawning behaviour of some char, which were taken from Jämtland and released in one of the Institute aquariums, the bottom of which was covered with stones and gravel.

Several of the instinctive actions belonging to spawning could be observed. In particular the courtship behaviour and aggressive behaviour of the male were studied and a number of observations could be made regarding the releasing stimuli for these actions. A part of the females' behaviour in connection with spawning could also be observed.

As was described in the previous report, FABRICIUS found that the char in the regulated lake Storsjouten, which normally spawn in the lake itself, migrated upstream to spawn in the mouths of the rivers after the damming-up. In order to study this phenomenon more closely FABRICIUS marked spawning char in the autumn of 1951 at five different places in another lake, Borgasjön, which is going to be dammed-up approximately 20 metres during the course of the coming year. The idea is to discover, by means of recoveries later on, partly if the same specimens which before the regulation spawned on skerries in the lake after the regulation may spawn in the stream, and partly if the char spawns at the same places year after year or if an exchange of fish occurs between the different spawning-grounds.

Whitefish. Marking and transplantation of whitefish from Vojmsjön to Skikkisjaure, where the whitefish has an extremely late spawning season as compared to the population in the first-mentioned lake, has continued in order to discover whether these transplanted females keep to their original spawning season or if this is influenced by the new environment.

Pike. FABRICIUS has also continued the study of pike spawning in the regulated lake Vojmsjön. Before the regulation spawning normally occurred at the time when the rising water reached the shore vegetation with the spring flood, usually about the middle of May. In the year 1951, when the regulation was made use of to the full extent, the time for the flooding of the shore vegetation was postponed for more than a month to the latter half of June. The pike then finally spawned before the water had reached the vegetation, but the spawning occurred three weeks later than usual. If there is a considerable delay in the high water level, the pike can, consequently, spawn without having access to vegetation. In an experiment carried out at the Institute in an aquarium, we succeeded here, as well, in getting pike to spawn on a bottom consisting of bare sand without any vegetation at all.

Speciation of Fish

Whitefish. NILS OLOV ÖSTERBERG could be employed, after a further grant from the National Science Research Council, for a greater part of 1951 for the continued working up of the extensive whitefish material. The autumn of 1951 was devoted amongst other things to the largest collection of whitefish samples up to the present from many lakes, special importance having been attached to the lakes in the south and middle of Sweden. The County fishery officials, especially Mr. LÜNING and Mr. SKOGLUND, were of the greatest

assistance in this respect. During the autumn and winter 1951—52 about 3,500 whitefish were collected. An account is given by SVÄRDSON at another place in this report of 94 spontaneous whitefish populations he examined.

It is of practical interest that an increasing amount of evidence has appeared to show that the whitefish species produce sterile or semi-sterile hybrids. Similarly there are indications that hybrids are often produced in great numbers if two species of whitefish are planted in a lake formerly devoid of whitefish. Where two sympatric species of whitefish have been living for a long time, the number of hybrids seems to be few. Probably the natural selection works in the direction of separating the species more and more effectively and preventing hybridization. The growth plays an important part in this connection because the whitefish have a tendency towards forming shoals together, individual size then playing a decisive rôle in the composition of the shoal.

The question, whether more than four species of whitefish exist in Sweden, has not been answered during the year but is still open.

Trout. The investigations carried out by ALM at Kälärne of different forms of trout and of the correlation in size and sexual maturity are being pursued. They show the previously-mentioned differences in colouration and in the sexual maturity of small river trout and big trout from the greater lakes. Sexual maturity is also reached earlier in individuals with better growth, and this good growth always persists in spite of spawning. The experiments also aim at finding out the length of life of the fish. In the autumn of 1951 there were 6 river trout F2, 14 years old, 10 of the same form 12 years old, and 7 Vätter trout, 12 years old, also in F2.

Hybrids. During 1951 ALM continued the hybridization experiments with salmon ♀×sea trout ♂, and sea trout ♀×salmon ♂ at the fish-culture stations at Mörrum and Älvkarleö. The results were varied but the hybridization experiments mostly showed greater mortality than the control experiments. Hybrids are still kept at Kälärne. Thus, in the autumn of 1951 there were 440 three-summer-old specimens of salmon ♀×sea trout ♂ with a length of 10—24 cm, and 430 three-summer-old specimens of sea trout ♀×salmon ♂, length 9—17 cm. The former hybrids seem, therefore, to have a better growth than the latter. In the salmon ♀×sea trout ♂-hybrids 2 males had ripe milt in the autumn of 1951. Several of these hybrids were rather silvery in colour, but the hybrids of sea trout ♀×salmon ♂ all had the parr-spots. The fry resulting from the 1950—51 experiments were kept in troughs at the fish-culture station at Kvarnbäcken. The mortality in all experiments was considerably greater among the hybrids than among the control fry.

The experiments to rear a second generation from bastards of char ♀×brook trout ♂ have yielded very poor results, in so far as most of these hybrids have died in their second or third year. New experiments are, however, still going on. The offspring of (char×brook trout) ♀×brook trout ♂ have

proved more satisfactory, as in the autumn of 1951 at Kälarne there were 86 three-summer-old specimens, 13—25 cm long, and 480 two-summer-old specimens, 6—17 cm long.

Relation between growth and sexual maturity in perch.

Population size	Ripe males		Average total length centimetres	
	number	percent	immature fish	ripe males
42	16	38.1	11.4	12.2
74	32	43.2	11.4	11.4
108	4	3.8	9.6	10.0
100	12	12.0	8.1	8.4
592	77	13.1	8.0	8.5
825	90	10.8	8.3	8.7

Perch. During 1951 ALM's studies at Kälarne of the relation between growth and sexual maturity have continued.

In the spring of 1951, when all perch in these experiments were 2 years old, several males, predominantly the larger ones, were ripe.

ALM publishes a paper in this report regarding earlier experiments with perch, both in ponds at Kälarne and in different lakes.

Studies in Regulated Lakes.

The trout population in five regulated lakes in the River Indalsälven has been under observation for a long period of time and RUNNSTRÖM gives an account of these investigations in a paper in this report. Owing to the damage done to the spawning-grounds and places where the trout grow up in the streams by their being laid dry or overdammed, the catch after the regulation has decreased. Extensive plantings of fry and one-summer-old fingerlings have not been able to compensate for the damage done to the population. The only way to eliminate the damage to a certain extent seems to be that a certain minimum water flow should always be allowed in the streams and that a fish ladder should be built in the cases, where the trout migrate down to the outflowing river for spawning.

Marking Experiments

The Institute acts as a centre for the marking experiments, which are carried out throughout the country. A record of the markings as well as particulars of the recoveries are sent in to the Institute and Dr. MIEZIS has filed all the marking hitherto done. The following table gives a summary of the markings carried out in the year 1951 and the recoveries reported that year. The salmon marking, carried out under the auspices of the Migratory

Species	Number of fish marked 1951	Number of recoveries 1951
Salmon	20,372	1,019
Sea trout	2,343	283
Trout	1,357	319
Char	2,685	1,833
Brook trout	4	2
Grayling	226	25
Whitefish	718	61
Pike	244	99
Pike perch	—	2
Perch	—	1

Fish Committee, comprised approximately 18,000 smolt, which were reared in ponds and were released at the mouth of rivers, where the spawning-grounds had been destroyed by the building of power stations.

Practical Studies of Fishing Gear

Nylon Experiments. Experiments to test the suitability of nylon thread in the manufacture of fishing tackle have been continued by MOLIN, the spun thread being mainly tested in different connections in the form of material tests and experiments with practical fishing. Thus nets made of different types of thread have been tested in Mälaren, Halmsjön and some lakes in Northern Sweden, the results having throughout given good catch figures as compared to cotton nets. In addition 2 large bow-nets made of French nylon thread were in use in Halmsjön.

Furthermore a preliminary experiment with manufacture and test fishing with nets, made of solid-drawn thread, was concluded. The catch results with this type of net were extremely good and should be followed, in spite of certain technical difficulties in the manufacture, by continued experiments with this type of thread, which probably will in certain respects be superior to the spun nylon thread.

Impregnation Experiments. These experiments have mainly comprised the testing of some new substances, which did not prove, however, to have an impregnating effect of any great value but were, on the contrary, worse than the average. In addition some staining experiments were made, and the most valuable result was that when impregnating with certain aniline substances with subsequent special staining, one obtains an impregnation effect at least as valuable as in impregnation with tanning-agents.

Publications in the Year 1951

The following papers by the staff of the Institute and other fishery biologists have been published during the year.

Rep. = Report from this Institute.

SFT = *Svensk Fiskeri Tidskrift* (Swedish Fishery Journal). Only Swedish language.

- ALM, G. The tagging of char, *Salmo alpinus*, LINNÉ, in Lake Vättern. *Rep.* 32: 15—31.
 — Fiskeriföreningar i Sverige år 1950. *SFT* 60: 23—25.
 — Åvaåns havslaxöringsbestånd. *SFT* 60: 158—159.
 — Sportfiskaren och fiskeribiologien. *Sportfiskaren* 17: 55—56, 68.
 — Åvaåns havslaxöringsbestånd och orsakerna till dess fluktuationer. Stockholms Sportfiskeklubb 25 år. Arn. Lundqvists Tr. Stockholm.
 — Laxfångsterna i Östersjön för närvarande ingen större fara för beståndet. *Ostkusten* (1): 27—31.
 — Modärn fiskevård. Några synpunkter på rationell fiskevård. »Fiske», Fiskefrämjandet, Stockholm.
- BRUNDIN, L., The relation of O₂-microstratification at the mud surface to the ecology of the profundal bottom fauna. *Rep.* 32: 32—42.
- FABRICIUS, E. The topography of the spawning bottom as a factor influencing the size of the territory in some species of fish. *Rep.* 32: 43—49.
 — Zur Ethologie junger Anatiden. *Acta Zool. Fenn.* 68: 1—178.
- GUSTAFSON, K.-J. Movements and age of trout, *Salmo trutta*, LINNÉ, in Lake Storsjön, Jämtland. *Rep.* 32: 50—58.
- LINDROTH, A. Ett exempel på den biologiska vattenundersökningens värde. *Vattenhygien* 7 (1): 21—23.
 — Fiskeribiologiska synpunkter på frågan om ytvattens renhet. *Vattenhygien* 7 (3): 49—55.
- MOLIN, G. Nylon contra cotton. *Rep.* 32: 59—65.
 — Nylon contra bomull. *SFT* 60: 44—48.
 — Fiskeredskapsimpregnering. *SFT* 60: 178—180.
- RUNNSTRÖM, S., Director's report for the year 1950. *Rep.* 32: 5—14.
 — The population of char, *Salmo alpinus*, LINNÉ, in a regulated lake. *Rep.* 32: 66—78.
- SVÄRDSON, G. The coregonid problem. III. Whitefish from the Baltic successfully introduced into fresh waters in the north of Sweden. *Rep.* 32: 79—125.
 — Om sikarnas arter och raser. *SFT* 60: 20—123.
- SÖRENSEN, I. An investigation of some factors affecting the upstream migration of the eel. *Rep.* 32: 126—132.
 — Om sambandet mellan vatten och jordförstöring. *Vattenhygien* 7: 1—13.
 — Försök rörande olika faktorerers inflytande på ålens uppvandringsförmåga. *SFT* 60: 98—101.
 — Kräftpesten 1951. *SFT* 60: 126—127.
 — Den statliga fiskeritjänstemannautbildningen. *SFT* 60: 160—162.
 — Kraftverksbyggnadernas inverkan på ålens vandringar. *Fångst og Fiske* 3: 1—9.
- TÖRNQUIST, N. Fiskar och fiske i Västergötland i Natur i Västergötland, Svensk Natur, Göteborg.
- TOOTS, H. Number of eggs in different populations of whitefish, *Coregonus*. *Rep.* 32: 133—138.
- VALLIN, S. Plankton mortality in the Northern Baltic caused by a parasitic water-mould. *Rep.* 32: 139—148.
 — The role played by *Didymosphenia geminata* (LYNGBYE) in clogging gill nets. *Rep.* 32: 149—152.

Year Class Fluctuations and Span of Life of Perch

By GUNNAR ALM

Contents

I. Introduction	17
II. Material and methods	18
III. Results	19
IV. Discussion	29
Year classes and span of life	29
Growth	31
Sex ratio and sexual maturity	33
Connection between year classes, growth, span of life and sexual maturity	34
V. Summary	37
VI. References	37

1. Introduction

It is known that in several species of fish, for example herrings, Baltic herrings, cod and whitefish, particularly extensive year classes occur certain years, and that such a year class can entirely dominate for several successive years. In a paper written in 1946 on the reasons for the origin of stunted fish populations, especially in perch (*Perca fluviatilis*), I have presented certain facts, which indicate that similar conditions sometimes occur here as well. In addition I have established in this paper that the perch are generally stunted in the small lakes of dystrophic type, which are so common in the morainic areas particularly in northern Sweden, whereas the growth is considerably better in oligotrophic and eutrophic lakes, where the perch consequently become larger. The idea has now been to follow during a greater number of years the composition of the stock of perch in a few different lakes of both types in order to shed light upon the question whether any greater changes in size arise during different years, how the different year classes appear, how long the normal span of life of the perch is, whether the commencement of sexual maturity has any influence on growth and span of life. An account of some of the results obtained will be given below.

II. Material and Methods

Fishing experiments have taken place in four lakes and certain experiments have been made in ponds. Three of the lakes are situated at the Kälärne Fishery Experimental Station in Jämtland, all of dystrophic type, partly surrounded by quagmires. They have been indicated as A 1, A 2 and A 3 with an area of approx. 2.0, 4.0, and 1.5 hectares, depth approx. 9.0, 10.5 and 6.0 m. All of them have very decided stratification, a bottom temperature during the summer of 4—5° C and a complete lack of oxygen here, a pH-value between 6—7 and a transparency of approx. 1.5, resp. 3.0 and 1.3 m. In the lakes A 1 and A 3 only stunted perch are to be found, in lake A 2 in addition also a few pike. In these lakes fishing only occurs now and then. The experiments have been on the largest scale in lake A 2. Experiments have also been made in a typical eutrophic lake in southern Sweden, called B, approx. 1,400 hectares, with all the species of fish characteristic for such lakes and profitable commercial fishing with a hectare yield of 5—10 kg/year. Experiments began in the year 1933 in lake A 1, in 1934 in A 2 and A 3 and in 1939 in lake B. They then continued up to and including 1945 in lake A 3, 1950 in lakes A 1 and B as well as up to and including 1951 in lake A 2.

In all these lakes, especially during the spawning season, intensive fishing has taken place and to a great extent measurements have been made of the length of the perch caught. The perch caught have in certain cases been put back in the lake, in other cases they have been removed. During the greater number of years sex classification has taken place, but often not of the whole material. Wire traps with different-sized mesh, as well as fike-nets and gill-nets have been employed for this fishing. The idea has been to obtain perch of different sizes, from the smallest spawning ones to the very largest. The length has always been measured from the tip of the snout to the tip of the tail fin. In some cases scale samples have also been taken for age analysis.

Marking has taken place in order to obtain a certain check on the specimens' span of life and to some degree their growth as well. This has been done by cutting off a certain fin, different ones for different years. Fin cutting in the case of perch, as the experiments in the ponds showed, is considerably more reliable than in other fish, as the fins do not grow again so easily. Such marking has taken place in all the four experimental lakes. Recovered marked perch have always been returned to the lake and could thus be captured during later years as well.

Pond experiments, which have been carried out at the Kälärne Fishery Experimental Station, have included rearing of both transferred perch from stunted populations and spawn from similar sources. The perch have had access to a rich fauna of diverse lower organisms in the ponds, which are

partly covered with vegetation. As a rule, in addition to the perch, other fish of about the same size were reared in the ponds. The perch have been examined every spring, sometimes in the autumn as well, with regard to their size, sexual maturity and spawning.

In numerous cases it has not been possible, however, to arrange the emptying of the ponds at the actual spawning season. Sometimes this has already partly occurred, in other cases it has been retarded. These experiments have, therefore, had to be supplemented, and extensive new experiments of this kind have been going on for the last few years.

From the comprehensive primary material, which has not been included, certain abridged tables (Tables 1—4) and graphical figures (Figures 1—4) are inserted in the following text.

III. Results

It appears from figure 1 that in lake A 2 during the years 1934—36 the usual length for the perch was 13—15 cm with the size increasing to a certain extent from year to year, indicating that here it was mainly a question of one or possibly a couple of rather good year classes. Smaller specimens belonging to new year classes were almost completely lacking the first two years. During the year 1936 a few such specimens were obtained from one or a couple of younger year classes, and during the years 1937 and 1938 specimens 9—13 cm in length were more common than larger specimens of 14—15 cm, even if many such specimens were still to be found. Obviously the removal of 2,000 specimens, which occurred during the years 1934—36, had considerably reduced the earlier year class or classes. It is certain, however, that the greater number of larger perch caught during subsequent years originate from here.

During the years 1937—38 only a few specimens were removed, but in spite of this the more usual length groups at that time did not play an important role in the future. At the same time a number of small specimens 6—7 cm in length now appeared, and in the year 1939 the greater part of the perch caught in the spring were 8—10 cm in length and, according to what was shown by examination as to age, 3 years old. This year class, which thus came into being in the spring of 1936, can now be followed during all the subsequent years with a certain increase of the most usual length, which during the spring of 1951 was 14—16.5 cm for these larger perch. Smaller-sized perch, which had been entirely lacking during the six years 1942—47, had however now appeared for several years. In the year 1948 occasional smaller specimens were thus to be found, which were quite distinct from the larger ones. In the years 1949 and 1950 the number of such specimens increased and in 1951 the smaller specimens of 9—12 cm

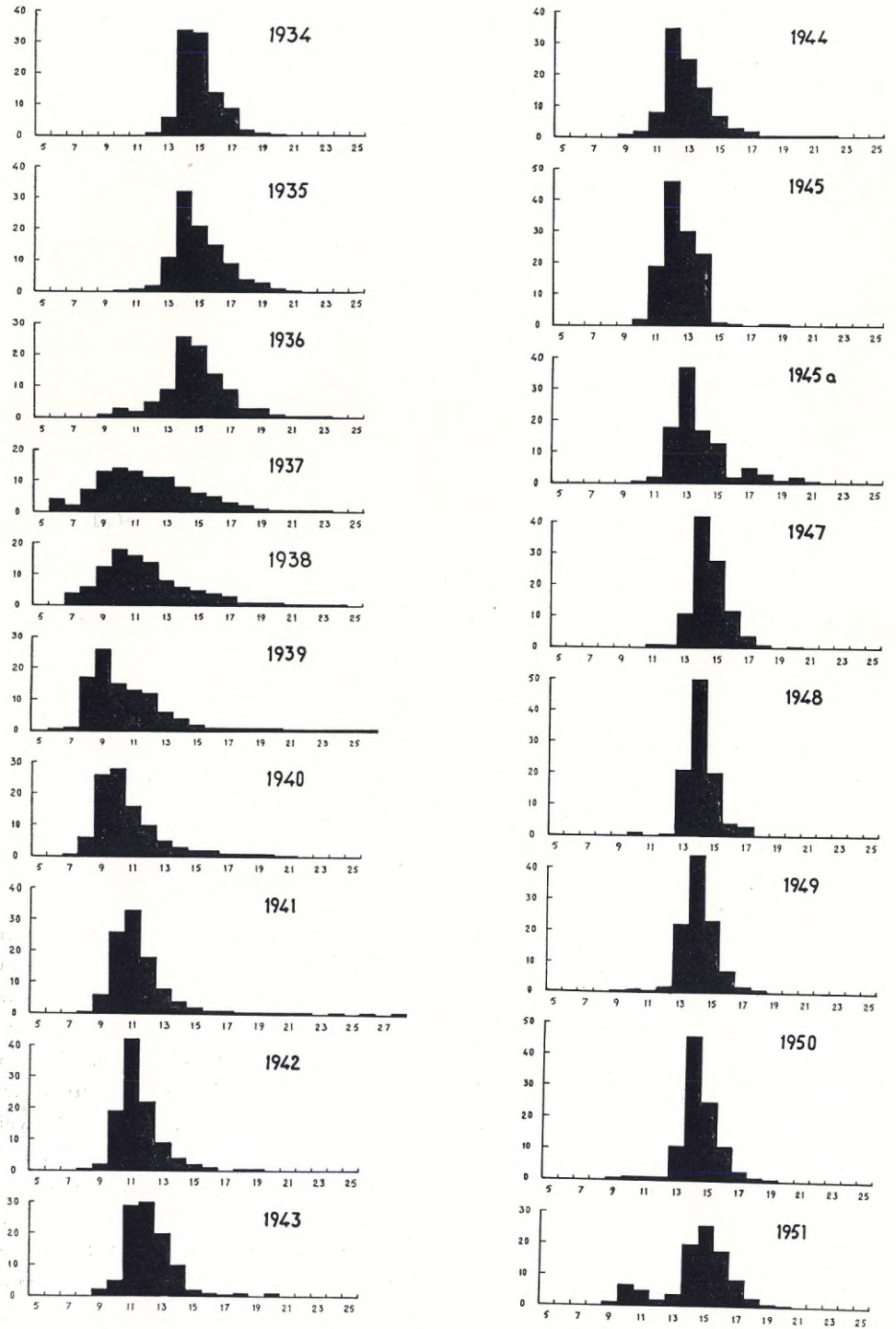


Fig. 1. Percentage distribution on different length groups in centimetres in lake A 2.

Table 1. Survey of the experiments in the lakes.

Year	Lakes															
	A 1				A 2				A 3				B			
	Number measured	Average length in cm ♂ + ♀	% ♂	Number removed	Number measured	Average length in cm ♂	Average length in cm ♀	% ♂	Number removed	Number measured	Average length in cm ♂	Average length in cm ♀	% ♂	Number removed	Weight in kg	Average weight in kg
1933	50	12.9	—	1,570	—	13.5	14.3	95.3	864	514	15.8	—	—	1,757	—	—
1934	526	12.1	—	526	1,244	13.5	14.3	95.3	864	357	15.0	—	—	1,183	373	0.22
1935	284	12.8	100	284	906	14.0	15.4	95.5	550	754	14.9	86.1	60	2,003	264	0.26
1936	1,080	12.2	—	1,080	1,299	13.7	16.2	86.5	600	1,003	14.7	94.6	150	1,721	445	0.26
1937	818	10.3	—	768	1,263	13.2	16.3	97.8	150	1,100	14.0	69.3	936	801	222	0.28
1938	1,649	10.9	96.0	878	1,326	11.4	16.1	97.1	150	886	13.6	83.7	348	853	185	0.22
1939	696	12.1	90.3	596	2,007	10.0	13.3	91.4	200	500	14.3	82.3	211	539	116	0.22
1940	327	10.9	53.3	100	2,203	10.2	13.1	90.7	100	754	12.0	93.0	605	1,383	303	0.22
1941	946	9.0	96.8	50	1,879	11.1	12.4	75.4	50	248	14.6	70.1	205	1,608	447	0.27
1942	1,842	9.2	91.4	50	1,192	11.1	12.3	80.9	85	293	15.2	51.8	25	656	153	0.23
1943	276	10.3	74.3	50	541	12.2	12.2	?	50	161	14.6	96.1	50	740	201	0.27
1944	726	10.9	75.5	166	4,003	12.2	13.8	54.0	3,362	82	14.4	—	—	970	219	0.23
1945	446	11.2	50.2	—	1,733	11.9	12.6	57.9	1,733	—	—	—	—	—	—	—
1945a	—	—	—	—	1,723	14.21	—	—	1,650	—	—	—	—	—	—	—
1946	—	—	—	—	—	—	—	—	—	—	—	—	—	1,332	402	0.30
1947	121	11.7	—	121	370	13.61	—	—	370	—	—	—	—	1,773	518	0.29
1948	—	—	—	—	271	13.5	14.3	59.4	271	—	—	—	—	717	188	0.26
1949	—	—	—	—	607	13.7	15.0	66.7	607	—	—	—	—	864	253	0.29
1950	1,104	11.4	67.8	1,104	541	14.2	15.6	80.9	—	—	—	—	—	850	225	0.28
1951	—	—	—	—	411	13.92	16.6	73.5	115	—	—	—	—	1,306	310	0.24
Total	10,891	—	—	—	23,143	—	—	—	—	6,655	—	—	—	12,583	—	—

¹ ♂ + ♀.² If only the bigger males from the year class 1936, are concerned, the mean length is 14.7 cm.

in length constituted 12.5 % of the entire total of perch caught. A clear division into two size groups can thus be proved now.

The sex ratio of the fish captured (Table 1) has varied considerably during different years. During the first years up to and including 1940 the males constituted about 90 % or more of the fish captured with spawning fishing. During certain later years 1944, 1945 and 1948 the males only constituted between 50 and 60 % of the fish caught at the spawning season. After that they increased once more in number and amounted to 73.5 % in the spring of 1951. It should be observed, however, that the two above-mentioned size groups behave differently, as the number of males was not as great among the larger perch, namely 68,4 % (236 ♂♂ and 109 ♀♀), while the smaller perch consisted entirely of males.

The average length of both sexes of the fish caught has been different, as is shown in table 1. The greatest difference occurred during the years 1937—1940. Then a relatively great quantity of larger specimens was found, all of which were females, and in addition a very great quantity of smaller specimens, most of which were males. Only 205 specimens (0.9 %) had a length of 20 cm or more of the grand total of 23,143 perch measured. The greatest length found among the specimens classified as to sex was 22 cm for the males (one specimen), 35 cm for the females (also one specimen). During the experiment the number of sexed perch of more than 20 cm in length amounted to only 9 males as against 44 females, most of which were, however, only just over 20 cm. Sexual maturity has generally occurred at a length of 8—9 cm in the males and 11—12 cm in the females or at resp. 2—3 and 3—4 years of age.

In the lakes A 1 and A 3 experiments have only been carried out to a limited extent (Table 1 and Fig. 2 and 3). The results can be summarized as follows. At the beginning of the experiments in lake A 1 the usual size was 12—15 cm. Here more than 2,000 specimens were removed during the first two years. The most usual size during the immediately following years was 10—12 cm. These perch as well, which clearly belonged to a new generation, were greatly reduced by means of intensive capture. The three subsequent years, 1937—39, the length increased once more. Now a larger number (more than 2,000) was once more removed, and during the year 1941 the larger specimens were almost entirely lacking. In their place numerous small specimens of 6—8 cm in 1940 and 7—10 cm in 1941 had once more appeared, and they now dominated with increasing length until the year 1945, when the usual size was 10—13 cm. No smaller specimens appeared during this time. To what extent this occurred during the subsequent years cannot be definitely determined. The length of the fish captured in 1947 and 1950 hardly suggests that any greater quantity of small specimens existed.

In the third experimental lake of the same type, A 3, the size was 14—

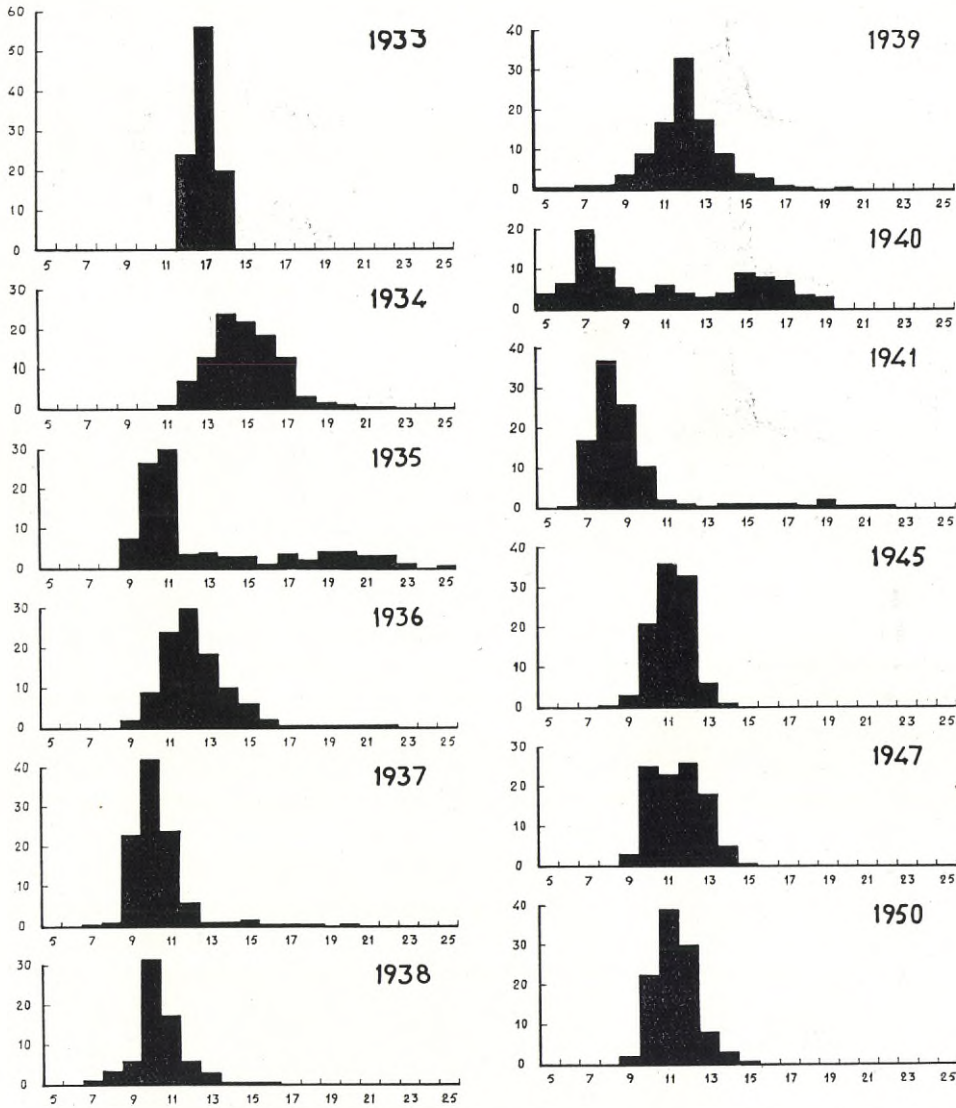


Fig. 2. Percentage distribution on different length groups in centimetres in lake A 1.

16 cm in the beginning. No great decimation took place for the first four years. The size was thus about the same, though with a somewhat increasing number of smaller specimens of 11—13 cm. It was not until the year 1939 that small perch of 7—8 cm appeared once more, introducing a new rich year class.

The sex ratio in lakes A 1 and A 3 was 90—100 % males at the beginning of the experiments. After that it fluctuated. In lake A 1 the number of males

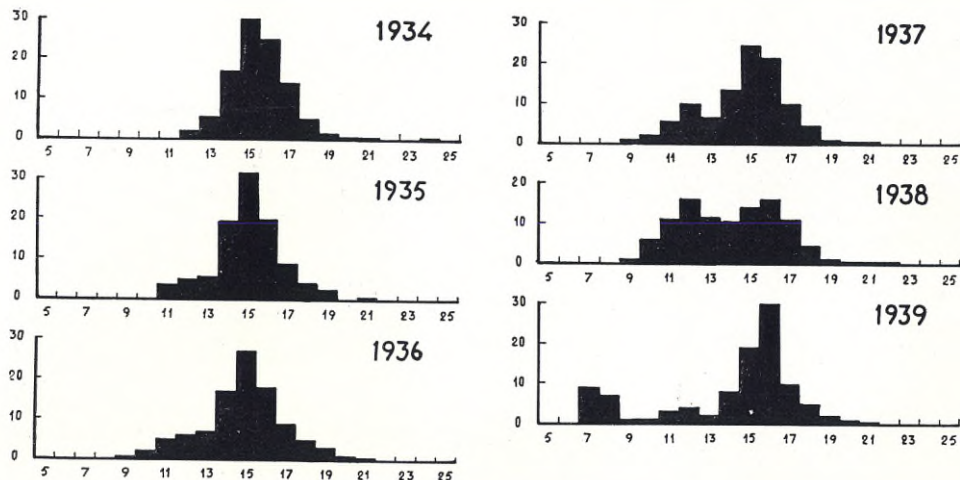


Fig. 3. Percentage distribution on different length groups in centimetres in lake A 3.

in 1941, when almost only small specimens were caught, amounted to 97 %, but it decreased during the following years to 50 % in 1945. Thereafter it increased once more to 68 % in the year 1950. In lake A 3 the percentage of males was high in the beginning, fluctuating later on.

In lake A 1 only 60 specimens of 10,891 perch measured (=0.6 %) attained a length of 20 cm or more, with the greatest length 25 cm in a female. The size in A 3 was somewhat better, inasmuch as of the 6,655 perch measured here 129 specimens (=1.9 %) had a length of 20 cm or more. 22 males and 44 females of the sexed perch attained this measurement. The greatest length was resp. 22 and 35 cm. In these lakes too the smaller specimens have mainly been males, the larger ones females. Size and age for sexual maturity (participation in spawning) have been about the same as in lake A 2.

The results from lake B present quite a different picture as regards size and sex ratio (Table 1 and Figure 4). During the first years 1939—1942 there was a good supply of large perch, 20—28 cm, of both sexes, belonging to several year classes, of which one at least was quite extensive. The fishing was good during 1941 and still better during 1942, and clearly the greater part of the above-mentioned rich year class was removed then. In 1943 large perch were namely no longer common, while numerous smaller specimens of 12—14 cm, principally males, dominated. Here it was obviously a new year class, which can be clearly followed during the years 1943—1945 with increasing length in both sexes. In 1947 and more plainly in 1948 new year classes appear once more, making themselves apparent in an abundant occurrence of small perch of 12—16 cm, and in the years 1949 and 1950

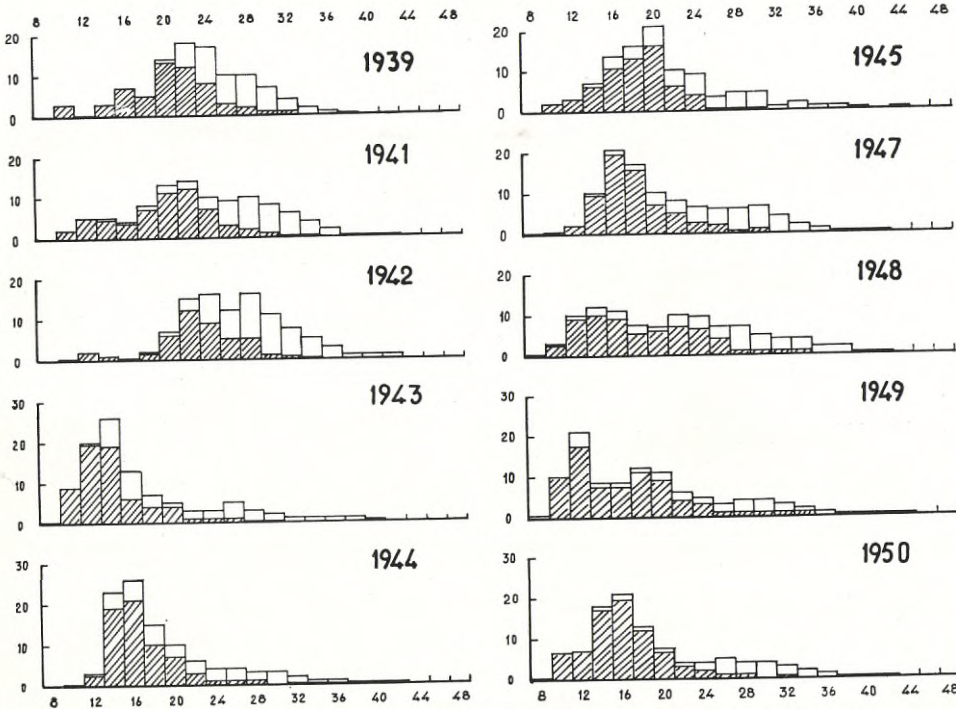


Fig. 4. Percentage distribution on different length groups in centimetres in lake B. Shaded part of bars indicates males, white part females.

still further year classes appear with numerous specimens even only 10—11 cm in length.

As far as regards the sex ratio the number of males in the year 1939 amounted to 57 % and in 1942 only 43 %. In the year 1943 the percentage of males increased considerably (74 %), after which it decreased once more to 62 % in the year 1948. The next year 1949 it had once more risen to 77 % and the following year was 76 %.

The difference in average length of the sexes in the perch caught, as table 1 and figure 4 show, was very noticeable every year. It was most marked in the years 1948—1950, when it amounted to more than 10 cm. In this lake, where length measurements solely comprised spawning and sexually classified perch, the greatest length for males was usually approx. 30 cm. Only 86 specimens (=1.0 %) of 8,207 males were thus 30 cm or more with a maximum of 35, 36 and 38 cm. On the other hand of the 4,376 females measured not less than 1,448 specimens (=33.1 %) attained the same length. As many as 259 specimens (=5.9 %) were more than 35 cm long, the largest 44 and 45 cm. The difference in size as compared to the A lakes is thus considerable. The smallest spawning females have been 10—12 cm, the males 8—9, but both in only very limited numbers. The more

Table 2. Survey of some marking experiments in the lake A 3.

	Marking years											
	1934		1935		1936		1937		1939		1940	
	Number marked and average length in cm											
	250	15.4	200	15.0	200	14.7	200	15.3	317	16.5	128	16.6
Number recaptured and mean length in cm in the first, second years, a.s.on after marking	17	15.4	88	15.3	80	15.7	67	15.8	136	16.7	105	17.4
	64	15.4	99	15.5	46	15.7	91	16.0	70	17.3	99	18.1
	78	15.9	73	15.8	37 ¹	15.8	57	16.6	65	18.0	36 ¹	17.5
	75	16.0	61	16.0	5	16.5	30	17.3	32 ¹	17.3	12	19.8
	73	16.2	70	16.8	2	17.3	29	18.4	5	19.6		
	33	16.7	20	18.2	10	18.2	20 ¹	18.3				
	12	16.9	20 ¹	18.5								
	25 ¹	18.5	4	18.4								
	10	17.9	3	19.0								
Total increase in mean length	—	3.1	—	3.5	—	1.1	—	3.0	—	0.8	—	0.9
Average increase per year	—	0.44	—	0.5	—	0.4	—	0.5	—	0.2		0.3

¹ Last year for recording of the length.

general size for spawning fish has been 14—16 cm for the females, corresponding to 3—5 years of age, and 10—12 cm for the males or 2—4 years of age.

Marking experiments in lake B have failed entirely. In the three smaller lakes of type A recapturing has been worst in lake A 2 and best in A 3, where a great number of perch were recaptured as late as 7 to 8 years after the year of marking, as may be seen in table 2. All the captured perch have been returned to the lake during these experiments, so the same specimens have undoubtedly often appeared again in the catch on several occasions. The percentage of perch recaptured is, as may be seen, high for the next few years, sometimes almost 50 %, in one case (1940 marking) 82 % during the first year and 77 % during the second. After five years recaptures amounted in some cases to 25 and even up to 35 %. The increase in length has fluctuated during the different years, but on the whole has been very inconsiderable.

Table 3 shows the size and increase in length of perch transferred in the spring of 1934 from lake A 2 to a pond as well as the same particulars for fry grown from spawn from this lake. In the spring of 1951 there were 6 specimens left from the first experiment, 2 males 33 and 34 cm long and 4 females resp. 28, 29, 36 and 38 cm in length. The mean length of all the

Table 3. Survey of some experiments in ponds.

Year	Perch transferred from lake A 2			Perch from spawn from lake A 2		
	Age (probable)	Number	Average length cm	Age	Number	Average length cm
1934	5	50	14.2	—	—	—
1935	6	28	16.8	—	—	—
1936	7	19	19.0	1	300	5.5
1937	8	19	21.8	2	500	8.8
1938	9	24	22.8	3	490	12.5
1939	10	21	24.2	4	348	16.0
1940	11	23	24.5	5	134	19.0
1941	12	23	25.1	6	110	21.1
1942	13	—	—	7	106	23.0
1943	14	19	27.5	8	89	24.1
1944	15	13	27.6	9	87	24.7
	16	7	29.1	10	41	25.3
1945	16	2 ♂	29.5	10	19 ♂	24.0
	16	5 ♀	29.0	10	22 ♀	27.0
1946	17	7	30.4	11	36	26.4
	18	6	30.8	12	31	27.3
1947	18	2 ♂	30.7	12	15 ♂	25.5
	18	4 ♀	30.8	12	16 ♀	29.1
1948	19	9	30.8	13	28	28.1
1949	20	7	32.1	14	27	28.5
1950	21	6	32.3	15	16	27.9
	22	6	33.3	16	15	28.9
1951	22	2 ♂	33.5	16	9 ♂	26.7
	22	4 ♀	32.8	16	6 ♀	32.2
	¹ 23	6	33.0	17	13	29.0

¹ autumn

specimens in the autumn of 1951 was 33.0 cm. These perch have thus lived 18 summers in the ponds. Probably they were at least five years old when they were transferred, so their age should now be a minimum of 25 summers. As opposed to their lake of origin they have grown well, especially during the first years. And this is the case for both sexes, although the females on the whole have been somewhat ahead. During later years their growth has been very slight. All of them, as far as could be ascertained, have spawned every year.

In the second experiment 15 specimens 16 summers old were found in the spring of 1951. 9 of these were males between 24 and 32 cm long (average length 26.7 cm) and 6 females 27—37 cm (average length 32.2 cm). The average length of all the specimens was 28.9 cm. Growth was somewhat better in the females from the beginning of sexual maturity, as is shown in table 4. Sexual maturity occurred at 2—3 years of age in the males, 3—5 years in the females, earliest in the specimens that grew most rapidly. Spawning has then occurred every year.

Table 4. Length in cm and sexual maturity in 3—6 years¹ old perch reared in ponds.

(Number of specimens in different length groups.)

Year, age	Sex	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	Total	Mean Length	
1938	♂	7	6	12	17	16	3	3	1	1	1																
3 years	...	♀			3	9	4	5	3	3	3																67	12.0
Sex not determ.			2	11	7	7	12	2	1																		30	14.6
																											42	11.6
1939	♂				10	33	46	52	22	6	7	2	1													179	15.6
4 years	...	♀					2	9	27	32	8	11	4	2	3	1	1										100	17.3
Sex not determ.						2	24	23	9	6	2	1	1	1													69	15.3
1941	♂							1	5	12	10	7	2	2	5	5	2									51	20.0
6 years	...	♀								1	8	6	6	6	5	5	3	6	3	7	2				1		59	22.5

¹ In the spring 1940 at 5 years age spawning had occurred before measuring.

² Probably most of these were females.

³ Probably all of these were females.

IV. Discussion

A. *Year Classes and Span of Life.*

The above-mentioned results show that the occurrence of rich and dominating year classes has been quite different in these experimental lakes. In lake A 2 one or perhaps two rich year classes were to be found at the beginning of the experiments and the following years as well as the last few years further new classes appeared. In addition to these there has only been one rich year class, originating in the year 1936, and it has been possible afterwards to follow it during the 12 years 1939—1951. The fact that it is really one single year class, without the addition of new ones, is shown partly by certain examinations of age, unfortunately only of a sporadic nature, but mainly because smaller specimens have not occurred in the lake during these years. If this had been the case, they should namely have been part of the catch in the same way as the year class in question was clearly noticeable already at a length of 8—10 cm. Perch of this length have only been caught the last few years and, as has been stated above, they belonged to new year classes.

The reason that no new rich year classes arose during the previous years can be sought in two directions. It can possibly be referred to unfavourable spawning conditions. However this can hardly have been the case every year. For many years spawning must certainly have taken place with good results in the form of growing fry and small fish. The destruction factor must, however, be added to this. The fry from new year classes have probably already at an early stage been eaten up by the older perch. Especially at the stage, when the fry abandon pelagic life and at a length of 1.5—2 cm make their way to the littoral region, they undoubtedly constitute a favourite food for the larger perch of 12—15 cm. The occurrence of the rich year class of 1936 has, therefore, certainly been a hindrance for the appearance of new year classes for many years. I have already previously (1946) advanced the theory that the lack of new growing year classes was the reason for the apparently mysterious state of affairs that in many lakes with a stock of stunted perch, nearly all the specimens have been of the same size and smaller specimens were nonexistent. This may be considered to be confirmed by the experiments now continued. First through the year class of 1936 being more and more reduced, primarily by the very great decimation in the years 1944—1945, small perch have begun to appear once more the last few years and have had a chance to grow up.

In both the other lakes as well the presence of a rich year class has constituted a hindrance for the appearance of new year classes. This hindrance was removed in lake A 1 by the immediate commencement of an intensive decimation of the stock, and almost at once a new generation followed. Renewed decimation of this one brought about yet another new

year class, which in its turn was very considerably reduced. Later on, after the decimation had ceased, however, no further rich year classes appeared. In lake A 3 inhibited decimation delayed the appearance of a new rich year class, and first at a much later date such a year class occurred.

It can thus be established that in lakes of type A new year classes in general do not appear in the years, when a previous rich year class is dominating. First when such a year class has been greatly reduced for different reasons (removal of fish, natural death), can the fry and the smaller fish from a new spawning grow up and give rise to a new rich generation. This is, of course, particularly evident, if the obstructive year class is very rich, and if the area of the lake is small.

A certain year class can dominate for a remarkably long period of time. This has, indeed, been the case in several of the examples now mentioned. The palm is taken, however, by the year class of 1936 in lake A 2, which is still dominating in the year 1951. The perch belonging to it have thus attained the high age of 15 years. Obviously in all these cases the natural mortality has been very low. The absence of predators (only a few pike) and freedom from competition with growing perch, which instead in the youngest stages constituted an addition to the diet of the older fish, have contributed to this. Clearly the physiological ageing has not entailed any great mortality. It should also be noticed that the percentage of males is large even when a year class has dominated for many years. The span of life must, therefore, have been great in both the sexes. This is also confirmed by the marking results. The high figure for recaptured fish for 6—8 consecutive years in lake A 3, where the majority consisted of males, shows that mortality was very low.

In lake B it has not been possible to indicate any corresponding long-lived dominating year class. Several year classes have succeeded one another here and each of them has constituted the greater part of the catch for a few years. Both removal from the lake (intensive commercial fishing) as well as natural mortality due to enemies and competition from new year classes have apparently brought about a shorter span of life in every year class. As a rule the perch have, therefore, not managed in any great number to become as old as in the lakes of the A type.

The reason that new demonstrable year classes have appeared far more often in lake B is undoubtedly first and foremost, because the fry from a good spawning season have had a chance to grow up without being decimated from the very beginning by larger perch or other kinds of fish. Here far richer plankton is to be found than in the lakes of type A, and in addition there is a good supply of roach, bleak and smelts. Fry and small fish of these species are more suitable food for the larger perch than its own fry. It is, therefore, more often spared, so for this reason as well new year classes can come into existence without hindrance. At the same time the

intensive fishing in such lakes with large perch must reduce the stock and contribute to shortening the span of life. And the large predatory fish found here such as pike and pike-perch, undoubtedly contribute to this decimation as well.

B. *Growth.*

As regards growth the following can be said with the support of previous investigations in the matter (ALM 1917, 1922, 1946, NILSSON 1921) and on a basis of the length measurements. (Table 1 and Fig. 1 and 2). In the A lakes the populations have always been stunted. This depends on the growth in these lakes decreasing very rapidly and gradually becoming extremely slow. The fact that this is the case under certain conditions has previously been established by the author (1946) and again recently by DEELDER (1951). No investigations in the matter have previously been made, however, for a greater number of successive years in the same lake. If in the lake A 2 the average length found during the different years is taken as an expression for the growth in the years, when the year class in question has been quite definite and separate, the following figures can be accepted. The average length for the males in the year 1939 was 10.0 cm and in the year 1951 (not counting specimens of 9—12 cm, which belong to new year classes) 14.7 cm. As far as the females are concerned the years between 1942 (when older and larger specimens began to decrease in number) and 1951 can be chosen with an average length of resp. 12.4 and 16.6 cm. The total average increase in length has thus been 4.7 cm for the males and 4.2 cm for the females, or 0.39 and 0.47 cm a year. During certain years the growth has been almost unnoticeable, whilst during other years it has been more evident. The latter was, for instance, the case during the year 1945. In 1944 3,360 specimens were removed, which quite naturally must have primarily included the larger perch of the rich year class. The next big catch in the spring of 1945 of 1,730 specimens in fact displayed a lower average length than the previous year. The remaining, now greatly reduced stock showed, however, a decided increase in growth during that year, so that the mean length in the autumn of 1945 was almost 2 cm more than in the spring of the same year. During the following year the increase in length was also marked in the females, probably in connection with the thinning out of the stock on account of old age and the great natural mortality accompanying it. The author has previously shown (ALM 1946) that such a reduction of the stock in a lake with a more favourable environment has resulted in better growth and increased size. It may be pointed out as a curiosity in this connection that the extremely great reduction of the stock of undersized perch in Lake Windermere (LE CREN 1944, WORTHINGTON 1950) does not seem to have resulted in increased individual size. Possibly there has still been keen competition for food here from increasing stocks of other species of fish.

Marking experiments also show quite a slight increase in growth. In spite of the marking not having paid regard to the individual specimens, one should namely be able to presume, owing to the great number of fish recaptured, that the average length found on the whole gives a true picture of the growth. This has varied in the recorded experiments between 0.3 and 0.6 cm per year. This approximately corresponds to the figures, which have been obtained in lake A 2 by comparing the average length of the year class of 1936 during different years. And it also agrees with the results, which have been obtained in both the other lakes. It is thus clear that, after the perch have attained a length of 12—13 cm, the growth in the great majority of specimens is very insignificant. Only occasional specimens especially females continue to grow and differ from the rest by being of larger size.

The reasons for the general poor growth, which seems to be the case in many stocks of perch, are undoubtedly many. First, of course, there is the scanty supply of suitable food, especially the absence of young fish of other species than perch, as well as other lower aquatic animals of a larger size such as *Gammarus* and *Asellus*, bigger larvae of insects and so on. The fact that larger perch do not eat smaller perch — apart from fry and very small fish — has been established by several scientists (ALM 1946, DEELDER 1951). It is also known that it is a characteristic phenomenon in many species of fish that the size of the particles of food has a certain significance for good growth. DEELDER (1951) has also shown that the perch's methods of hunting and opportunity for the fish prey to find protection in existing vegetation play an important part as regards the possibilities for the perch of 14—15 cm in length having access to fish food and thereby increased length. OLSTAD (1919) has, however, considered that a stunted population is caused by natural mortality commencing early, while the growth itself would be about the same in these and the big stock. The experiments now discussed show that this is not the case.

The majority of scientists, who have studied the growth of the perch, have pointed out that the males grow less and that they do not become as big as the females. This is, in fact, the case here. The difference is, however, quite slight in the A lakes, which is connected with the poor growth on the whole. The average length of the sexes in the catches and the difference in this respect are, of course, not an expression for the dissimilar growth of the sexes, as, for example, during several of the years in question different year classes have been included. During certain years, on the other hand, when the size of the fish caught has been more concentrated on account of only a single extensive year class, and when neither larger nor smaller specimens play any great part, one seems to be able to suppose that the difference in the mean length of the sexes on the whole reflects the difference between them in growth. This now amounts to 1 to 2 cm. If in the year 1951 regard is only paid to the larger, more common

length groups of 13 cm and more, which belong to the above-mentioned year class, the mean length amounts to 14.7 cm for the males and 16.6 cm for the females. Both males and females have continued to grow, though, even if the increase in size has been very small. It has thus not been possible to find any difference between the sexes in this respect, contrary to HUITFELDT-KAAS's (1927) view, that the males more generally finish growing at a lower age than the females.

Even if it has not been possible in lake B to follow a certain year class for more than a few years, it is obvious, nevertheless, that the perch's growth has been far better here than in the A lakes. An increase in length of several cm per year is quite normal in this lake as it is in other lakes of the same type, particularly as far as the females are concerned. Primarily this good growth depends on a plentiful supply of food and, moreover, suitable food. Sufficient plankton for the smaller perch and various lower species of animals of different kinds as well as fish, especially roach and smelts, for the larger perch, make continued good growth possible here even at a greater age. In this case the difference in size between the males and females appears far more clearly than in the A lakes. In lake B, where the year classes merge more closely into one another, one can only in certain years suppose, that the mean length of the fish caught reflects the difference in growth of the sexes at the same age. This is possibly the case in the years 1939—1942 and 1944—1945. The males were then on an average 6—9 cm smaller than the females.

C. *Sex Ratio and Sexual Maturity.*

The males are predominant in the smaller size groups in all the lakes. This is connected with the earlier occurrence of sexual maturity in this sex. A growing rich year class is thus first evident by a plentiful occurrence of small spawning males, for which reason the percentage of males in the spawning stock must be particularly high during such years. This was, indeed, the case in lake A 2 during the years 1937—1938 and 1950—51. During the year 1951, for that matter, all the perch up to and including 12 cm in length, previously mentioned as belonging to a new year class, were males. A curious feature is the high percentage of males in the A lakes the first years experiments were made as compared to the latter half of the 1940's. Probably this depends on the males being more agile than the females and thus easier to catch. After several years' removal the relative number of males should then decrease, unless a new year class appears. This has, in fact, been the case. The percentage of males decreased, for example, in lake A 2 from 1935 to 1936, and the same thing happened to the year class of 1936 during the years 1939—1948, before the small specimens from a new year class began to appear in the years 1949—1951.

The same conditions have prevailed in the lakes A 1 and A 3. LE CREN (1944) has also established by the decimation experiments in Lake Windermere that the number of males in the catches was at first very great, but decreased in connection with the considerable quantity of fish removed from the lake. The often great preponderance of males in the spawning does not depend, however, on a real preponderance. When fishing at other times of the year than the spawning season the sex ratio, as my previous investigations have shown, is about 50 : 50, and the same applies to the small fish reared in ponds (Table 4).

In lake B the number of males was particularly great during the years 1943, 1949 and 1950, here too in connection with an extensive occurrence of small specimens from new rich year classes. The preponderance of males is never as great in the catches in lakes of this type. This depends partly on larger perch only being caught as a rule. It can also be partly connected with the greater agility of the males, as previously mentioned, whereby they more easily become the victims of predatory fish. Their smaller size must also contribute.

Regarding the occurrence of sexual maturity, it is, of course, difficult to determine this with exactitude in nature, inasmuch as it is not easy to catch the smallest spawning specimens in the fishing-year. The information given above indicates that in both the lakes sexual maturity began to occur at about the same age, 2—3 years for the males and 3—4 years for the females, though somewhat later in lake B, where the length has been greater at the same time. In order to investigate more closely the time for the commencement of sexual maturity in populations with different growth, and how the commencement of sexual maturity affects continued growth, direct experiments in the matter have been going on for several years at Kälärne. The results will be published at a later date.

D. Connection between Year Classes, Growth, Span of Life and Sexual Maturity.

The following can be established from a comparison of the now discussed results from different types of lakes. In lakes of dystrophic type, especially characteristic for the northern parts of the country, new rich year classes of perch appear more seldom. A certain rich year class is often dominant, however, for a long sequence of years, for which reason the perch's span of life is great here, clearly in many cases 10—15 years, and this applies to both sexes. The growth is poor, on the other hand, and the individual size small, usually 12—15 cm. Only a few specimens, mostly females, attain a length of 20 cm or more. For many years the stock of perch in such a lake can, therefore, consist mainly of rather similar-sized specimens of the same age, while both smaller (younger) and larger specimens are lacking or only occur sparsely.

In lakes of eutrophic type, and according to earlier investigations also in lakes of oligotrophic type, new rich year classes appear far more often, sometimes several consecutive years. A certain year class is seldom dominant then for any great length of time, at the most a few years, and the span of life is therefore not as great. Growth, on the other hand, is good, and the perch are generally big and usually attain a length of 20—30 cm, numerous specimens, particularly females, 35—40 cm. The stock of perch in such lakes consists in the majority of cases of specimens of a number of different sizes of varying ages. Sexual maturity occurs as a rule at a somewhat higher age here than in the stunted populations.

These facts seem at the first glance to indicate that a certain connection exists between on the one hand a long span of life, poor growth and possibly earlier sexual maturity and on the other hand shorter span of life, good growth and possibly later occurrence of sexual maturity. In this connection it should also be mentioned that American scientists (HARKNESS 1922, SCHNEEBERGER 1935) have pointed out that perch in such lakes, where the growth is poor, attain a greater age (8—9 years) than in the lakes with good growth. It is, however, remarkable in this connection that the perch in North American lakes are often of a very low age (JOBES 1933, ESCHMEIJER 1937, 1938, HILE 1942) and seldom become older than 8—10 years, or most often not more than 6 years (Parson 1950). In this respect there are great differences as compared to the Swedish lakes. Regarding the commencement of sexual maturity no definite information exists. Apart from the different span of life in Europe and America, the connection between age and type of growth appears, however, to be similar in character.

It has been established, however, in species of fish of the salmon and whitefish families (FOERSTER 1947, RICKER 1950, SVÄRDSON 1951) that bad growth in stunted populations of the above-named species is connected with low age and early sexual maturity. Finally it has been found in the aquarium fish *Lebistes* (SVÄRDSON 1943) and in perch (ALM 1946, OLSTAD 1919) that sexual maturity occurs earlier with very good growth than with moderately good, but that very unfavourable environmental conditions cause early sexual maturity and slower growth and, in addition, according to SVÄRDSON (1951) a lower age as well. The conditions seem, therefore, to be rather complicated.

The present results from the experiments with perch indicate, however, that it is primarily the milieu and the nature of the biotop, which are the reason for the only apparent connection between growth and span of life (age). The results from the pond experiments thus show that good growth is by no means incompatible with great age. This transplantation of stunted perch to another, undoubtedly more favourable, biotop occasioned an immediate increase in growth, amounting during the first three years to an average of 2—3 cm per year and after that varying greatly, but sometimes 1 cm or more per year. In the spring of 1944, when these perch were probably

of the same age as the year class of 1936 were in lake A 2 in the spring of 1951, namely 15 years, the mean length was 27.6 cm or about 12.5 cm more than the perch of the same age in the lake. The perch in the other pond experiment, as well, have both grown well and attained a great age, namely 17 summers. Even if mortality has been quite high in these experiments during certain years, about 50 % of the transferred perch were left after 7 years, and of those, which then survived, some remained alive for a further 10 years. And the perch reared from fry in the ponds have had a very low death-rate for many years, if one disregards the first years with their often considerable losses.

The following statement can, therefore, be made. As the perch in the stunted populations in the natural lakes attain a great age, and as this is also the case with the stock of perch raised in the ponds, but with good growth, the growth and the span of life cannot, consequently, be directly dependent on one another. The large-sized population as well in natural lakes ought also to be capable of attaining in all probability the same great age as the stunted populations. But as the large-sized populations are partly subjected to profitable fishing, partly occur in lakes of a richer biotope with a number of species of fish, intensive fishing, numerous enemies and keen competition must entail, as has been mentioned above, a considerable reduction of these populations and thus lower the age. It is possible that if these factors which increase mortality did not exist, the span of life in these large-sized populations would be just as long and perhaps longer than in the stunted populations. If that is so the somewhat earlier commencement of sexual maturity may perhaps be connected with poorer growth and shorter span of life. In which case it would correspond to what has already been mentioned above regarding the undersized and large-sized salmon and white-fish stocks.

The earlier commencement of sexual maturity in the males than in the females does not seem to entail in the case of the perch any greater mortality and lower age in the males. Even if the growth in the males becomes somewhat poorer than in the females in connection with the commencement of sexual maturity, the results of the experiments cannot be interpreted as showing any greater natural mortality in the former. In the very old year class in lake A 2 males were still common. This was also the case in the pond experiments with rearing of perch from fry.

The new experiments now going on at Kälarne, which have been previously mentioned, are intended in particular to shed light on this and the other questions discussed above regarding the connection between growth, sexual maturity and span of life. I hope, therefore, to be able to return in a few years time with new viewpoints on these problems, which are of great practical importance.

V. Summary

The populations of perch in lakes of dystrophic type are mostly stunted. This depends on the growth at a length of 11—12 cm becoming extremely slight and almost ceasing during certain years. New rich year classes only appear during such years, when already grown rich year classes are lacking. A rich year class can be entirely dominant during a long sequence of years, the longest case now recorded being 15 years, when both males and females seem to attain the same high age.

In lakes of eutrophic type the populations of perch are usually large-sized and growth continues even at a greater age. New rich year classes often arise, although not every year. A rich year class dominates for only a few years. Here the span of life is often not as long.

In all populations the males become sexually mature 1 to 2 years earlier than the females. The former then grow somewhat less, and the difference in size between the sexes becomes greater the better the growth is in the population as a whole. Among spawning specimens males are in the majority amongst the smaller length groups, females in the larger length groups. No demonstrable dissimilarity in the span of life in the sexes is to be found.

The sex ratio is normally 50 : 50, but at the spawning season and especially in the stunted populations more males are always caught than females, sometimes up to 100 per cent males.

No correlation exists between growth and span of life. The natural mortality is low both in the stunted populations in lakes and in the large-sized populations in ponds. The reason for the low age in the large-sized populations in lakes is probably intensive fishing, death caused by predators and intra- and interspecific competition.

VI. References

- ALM, G. 1917. Undersökningar rörande Hjälmarens naturförhållanden och fiskar. *Medd. K. Lantbruksstyrelsen* Nr 204: 1—112.
- 1922. Bottenfaunan och fiskens biologi i Yxtasjön. *Medd. K. Lantbruksstyrelsen* Nr 236: 1—186.
- 1943. Beiträge zur Kenntnis der Limnologie kleiner Schwinguferseen. *Arch. f. Hydrobiol.* 40: 554—575.
- 1946. Reasons for the occurrence of stunted fish populations with special regard to the perch. *Rept. Inst. Freshwater Res. Drottningholm* 25: 1—146.
- BRÖFELDT, P. 1915. Om fiskarne och fiskeriförhållandena i Thusby träsk samt anvisningar till dessas förbättrande. *Finlands Fiskerier* 3: 106—123.
- CREN, E. D. LE. 1944 Perch and perch fisheries. *Ann. Rep. Freshwater Biol. Assoc. Brit.* 12: 13—16.
- DEELDER, A. 1951. A contribution to the knowledge of the stunted growth of perch in Holland. *Hydrobiologia* 3: 357—378.
- ESCHMEYER, R. W. 1937. Some characteristics of a population of stunted perch. *Pap. Mich. Acad. Sci. Arts and Lett.* 22: 613—638.

- 1938. Further studies of perch populations. *Pap. Mich. Acad. Sci. Arts and Lett.* 23: 611—631.
- FOERSTER, R. E. 1947. Experiment to develop sea-run from landlocked sockeye salmon. *J. Fish. Res. Bd. Can.* 7: 88—93.
- HARKNESS, W. J. K. 1922. The rate of growth of the yellow perch in Lake Erie. *Univ. Toronto Stud. (Biol. Ser.) Publ. Ontario Fish. Res. Lab.* 20. VI: 88—95.
- HILE, R. and JOBES, F. 1942. Age and growth of the yellow perch in the Wisconsin waters of Green Bay and Northern Lake Michigan. *Pap. Mich. Acad. Sci. Arts and Lett.* 27: 241—266.
- HUITFELDT-KAAS, H. 1927. Studier over Aldersforholde og Veksttyper hos Norske Ferskvannfisker. Oslo.
- JOBES, F. 1933. Preliminary report on the age and growth of the yellow perch from Lake Erie, as determined from a study of its scales. *Pap. Mich. Acad. Sci. Arts and Lett.* 17: 643—652.
- JÄRNEFELDT, H. 1921—23. Untersuchungen über die Fische und ihre Nahrung im Tuusulasee. *Acta Soc. Fauna Flora Fenn.* 52: 1—160.
- LINDHÉ, C. 1942. Djupens randiga rovriddare. Wahlström & Widstrand.
- NILSSON, D. 1921. Några insjöfiskars ålder och tillväxt i Bottniska viken och Mälaren. *Medd. K. Lantbruksstyrelsen Nr 231: 1—56.*
- OLSTAD, O., 1919. Undersökelse over Abborr. Fiskeriinspekt. Indberetn. Kristiania. 1—40.
- PARSONS, J. W. 1951. Growth studies of the yellow perch in three northwest Iowa lakes. *Iowa State Coll. Sci. Journ.* 25: 495—500.
- RICKER, W. E. 1950. Cycle dominance among the Fraser Sockeye. *Ecology* 31: 6—26.
- SCHNEEBERGER, E. 1935. Growth of the yellow perch in Nebish, Silver and Weber Lakes, Vilas County, Wisc. *Trans. Wisc. Acad. Sci. Art and Lett.* 29: 103—130.
- SVÄRDSON, G. 1943. Studien über den Zusammenhang zwischen Geschlechtsreife und Wachstum bei Lebistes. *Rept. Inst. Freshwater Res. Drottningholm* 21: 1—48.
- 1951. The coregonid problem. III. Whitefish from the Baltic successfully introduced into fresh water in the north of Sweden. *Rept. Inst. Freshwater Res. Drottningholm* 32: 79—125.
- WORTHINGTON, E. B. 1950. An experiment with populations of fish in Windermere, 1939—48. *Proc. Zool. Soc. London V.* 120: 113—149.

Zur Kenntnis der Taxonomie und Metamorphose der Chironomidengattungen *Protanypus* KIEFF., *Prodiamesa* KIEFF. und *Monodiamesa* KIEFF.

Von LARS BRUNDIN

Wie bekannt spielen die Larven der Gattungen *Protanypus* und *Monodiamesa* bei der Charakteristik der Tiefenfauna europäischer Seen eine wichtige Rolle. Generell genommen sind sie als Indikatoren eines oligotrophen, sauerstoffreichen Milieus zu betrachten. Es ist aber lange ein fühlbarer Mangel gewesen, dass von den seebewohnenden Arten dieser Gattungen bisher nur die Jugendstadien von *Monodiamesa bathyphila* KIEFF. und *Protanypus morio* ZETT. bekannt sind (THIENEMANN 1918, bzw. LENZ 1925). In vielen Fällen war es deshalb nicht möglich, die gefundenen Jugendstadien von *Monodiamesa* und *Protanypus* bis zur Art zu bestimmen. Eine weitere Ursache hierzu war auch die ungenügende Kenntnis der Imagines der in den Seen des Alpengebietes lebenden *Monodiamesa*- und *Protanypus*-Arten. Das Studium des mir nun vorliegenden Materials hat hier in mehrfacher Hinsicht Klarheit gebracht.

Protanypus caudatus EDW.

Imago: EDWARDS 1924, S. 122; GOETGHEBUER 1939, S. 24, Tafelfig. 43.

Larve: Nicht sicher bekannt, aber von der *morio*-Larve wahrscheinlich nicht trennbar.

Puppe: Von der sehr ähnlichen *morio*-Puppe durch folgende Merkmale abweichend: Exuvie durchschnittlich kleiner, Länge 8,5—10,5 mm, und durchschnittlich viel dunkler gefärbt, meistens dunkelbraun (bei *morio* immer gelb). Die beiden sekundären, mehr analwärts sitzenden Frontalhöcker sind sehr klein und niedrig, wie bei *forcipatus* (Abb. 11), während sie bei *morio* ebenso gross wie die beiden vorderen Höcker sind. Das Thorakalhorn (Abb. 5, 6) ist kleiner und schmaler, Länge 0,45—0,60 mm, sehr regelmässig zylindrisch, ganz distal mit kleinen Spitzen bewehrt und etwa 11—14 mal länger als breit (bei *morio*, Abb. 2, 3, dagegen einen meistens etwas unregelmässig geformten, von den Seiten mehr oder weniger zusammengedrückten, 0,60—0,80 mm langen Schlauch bildend, der ganz ohne

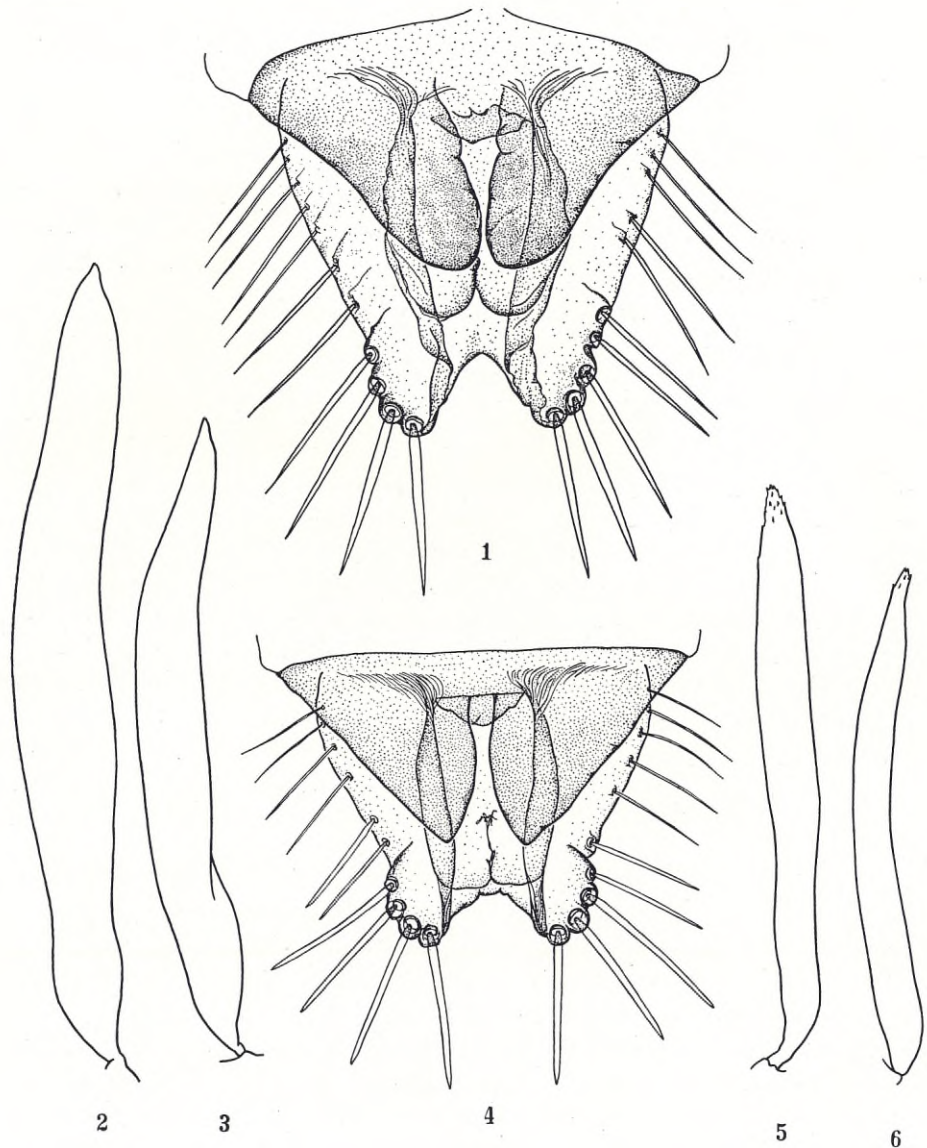


Abb. 1—3. *Protanypus morio*. Hinterende der ♀-Exuvie, ventral (Abb. 1); Thorakalhorn einer Puppe aus dem See Innaren in Småland (Abb. 2) und aus dem See Torneträsk in Schwedisch-Lappland (Abb. 3). — Abb. 4—6. *Protanypus caudatus*. Hinterende der ♀-Exuvie ventral (Abb. 4); Thorakalhorn der Puppe: Jämtland, Stora Blåsjön (Abb. 5—6).

Spitzen ist). Das Chagrin der Abd. Segm. ist viel schwächer entwickelt als bei *morio*; Segm. I und II sind praktisch genommen glatt, an III—V kommen Chagrinspitzen nur oralmedian vor, an VI und VII gibt es chagrinierte Partien sowohl oral- wie analmedian; Segm. VIII ist ziemlich gleichmässig chagri-

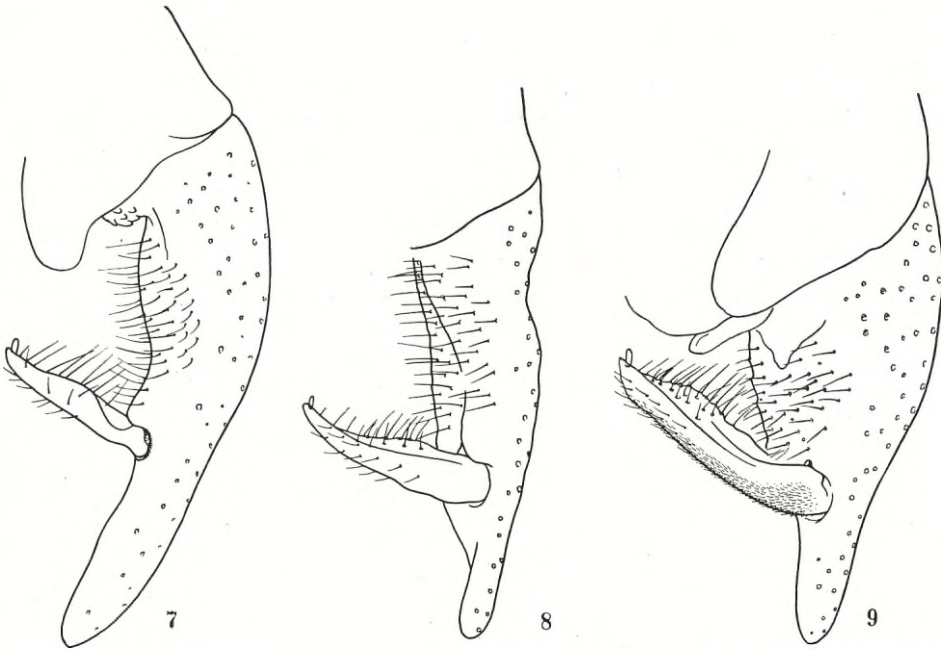


Abb. 7—9. Lateralansicht des Hypopygs von *Protanypus caudatus* (Abb. 7), *P. forcipatus* (Abb. 8) und *P. morio* (Abb. 9).

niert. Die Chagrinspitzen sind durchgehend kleiner als bei *morio*. Bei dieser Art besitzen alle Abd. Segm. ein gleichmässiges, nur an den Seiten fehlendes Chagrin. Die dorsalen Borsten sind bei *caudatus* länger und auch in grösserer Zahl vorhanden als bei *morio*. Bei *caudatus* gibt es auf jedem Segm. jederseits der Medianlinie 12—17, bei *morio* 8—11 Borsten. Die Zahl und Stärke der grossen lateralen Borsten des Analsegmentes sind bei beiden Arten sehr variabel und liefern keine trennenden Merkmale. Dagegen ist die Ansatzpartie der distal sitzenden, besonders kräftigen Lateralborsten bei *caudatus* durch eine Einschnürung besonders markiert, während bei *morio* eine solche Einschnürung meistens kaum angedeutet ist (vgl. Abb. 1 und 4). Gute Merkmale bieten die grossen ventralen, beim ♂ einfachen, beim ♀ doppelten Zipfel des VIII. Abd. Segmentes, die bei *caudatus* scharf zugespitzt, bei *morio* aber breit abgerundet sind (Abb. 1 und 4).

Die vorliegenden *caudatus*-Häute wurden im nördlichen Jämtland von A. MÄÄR gesammelt: Stora Blåsjön 25.6.49, eine Haut; Ströms Vattudal 7.9.49, 2 Häute; vor Strömsund (zwischen Ströms Vattudal und Russfjärden) 20.5.49, zahlreiche Häute. Die spezifische Identität konnte durch den Fund eines Männchens mit noch festsitzender Puppenhaut (vor Strömsund am 20.5.49) einwandfrei festgestellt werden. Die Fangdaten der Häute ergänzen unsere Kenntnis der Phänologie der Art. Sie zeigen nämlich, dass

die erste Generation in den schwedischen Gebirgsseen eine ziemlich lange Schlüpfungsperiode hat, die sich von Ende Mai bis Anfang Juli erstreckt (vgl. BRUNDIN 1949, Tab. 106).

Die *caudatus*-Häute sind meistens schon makroskopisch durch ihre dunkelbraune Farbe erkennbar. Die auf dem Stora Blåsjön am 25.6.49 gefundene Haut ist aber überraschenderweise etwa gleich hell wie die *morio*-Häute. Entscheidend wird deshalb in erster Linie der Bau der Frontalhöcker, der Thorakalhörner und der ventralen Zipfel des VIII. Abd. Segmentes.

Imagines sind bisher bekannt aus Gebirgsseen in Norwegen: Tyin-See (loc. cl., EDWARDS 1924) und Schweden: Jämtland (BRUNDIN 1949, S. 719), Lappland, See Rissajaure zwischen Abisko-Riksgränsen (leg. BRUNDIN 1950).

Protanypus forcipatus (EGG.) BRUND.

Die Identität dieser von EGGER schon im Jahre 1863 aus Gmunden in Oberösterreich beschriebenen *Protanypus*-Form ist bisher unsicher geblieben. GOETGHEBUER (1939, S. 24) glaubte sie mit *caudatus* EDW. aus Norwegen identifizieren zu können, aber PAGAST (1947, S. 561) ist in seiner *Diamesa*-Monographie der Ansicht, dass dies noch an der Hand von weiterem Material zu überprüfen ist.

Protanypus-Larven sind seit langem aus dem Lunzer Untersee bekannt (LENZ 1925). Später sind weitere Larvenfunde aus anderen Alpenseen hinzugekommen: Eibsee, Starnberger See, Ammersee, Walchensee, Plansee, Bodensee, Weisser See in Kärnten (PAGAST 1947, THIENEMANN 1950). Da weder reife Puppen noch Imagines vorlagen, waren aber diese Larven nicht näher bestimmbar.

Nun erwähnt aber PAGAST (l.c., S. 508) eine *Protanypus*-Exuvie aus dem Starnberger See in Bayern, die sich von jener bei *morio* u.a. durch das viel schwächer entwickelte Chagrin der Abd. Segm. unterscheidet. Er vermutet, dass es hier von einer anderen Art die Rede ist.

An der Hand einer ihm vorliegenden reifen ♂-Puppe aus dem Lunzer Untersee identifizierte THIENEMANN (1949, S. 147) die *Protanypus*-Population dieses Sees als *morio*.

Es schien demnach, als ob wir im Alpengebiet mit zwei *Protanypus*-Arten zu tun hätten: *morio* und *forcipatus*, und die Frage, ob *forcipatus* mit *caudatus* identisch wäre, stand noch offen.

Während einer Alpenreise im Spätsommer 1949 gelang es mir, an einem kleinen See im Grimselpass (2 165 m) in der Schweiz ein ♂ und eine Exuvie einer *Protanypus*-Art zu erbeuten. Als ich dann durch das Entgegenkommen Professor THIENEMANNS Gelegenheit hatte, sowohl die fragliche ♂-Puppe wie ein reiches Exuvienmaterial aus dem Lunzer Untersee zu untersuchen, konnte festgestellt werden, dass das Grimsel- und das Lunzer-Material einheitlich

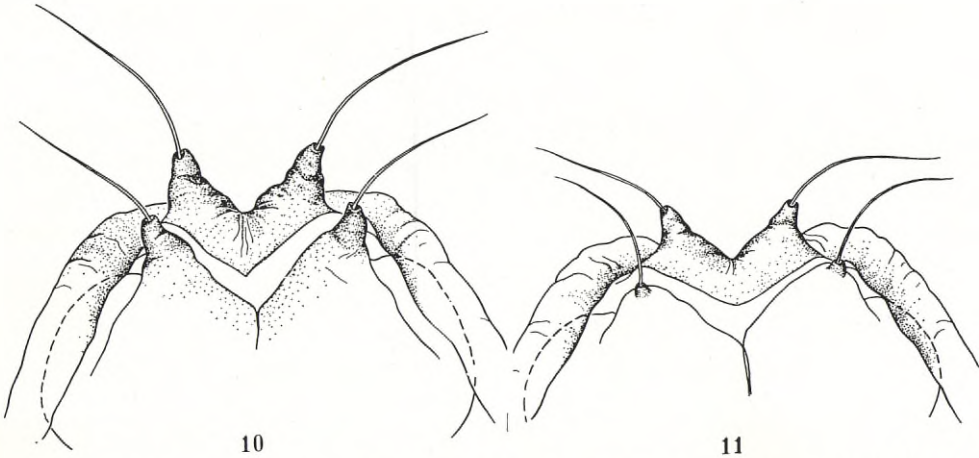


Abb. 10—11. Vorderende der Exuvie bei Dorsalansicht von *Protanypus morio* (Abb. 10) und *P. forcipatus* (Abb. 11).

war und einer Art vertrat, die weder mit *morio* noch mit *caudatus* übereinstimmte. Nach der Beschreibung konnte ebenfalls nicht bezweifelt werden, dass die von PAGAST auf dem Starnberger See gefundene Exuvie hierher zu stellen ist. Es scheint klar, dass wir es hier mit dem echten *forcipatus* zu tun haben.

Höchstwahrscheinlich sind die nördlichen Arten *morio* und *caudatus* in den Seen der Alpen überhaupt nicht vertreten. *Protanypus forcipatus* ist am nächsten mit *caudatus* verwandt und bildet zusammen mit diesem ein typisches borealpines Artenpaar. Dagegen scheint es sehr wahrscheinlich, dass die *Protanypus*-Larven des polnischen Wigry Sees (ZAVREL 1926) zu *morio* gehören.

Imago: Von *caudatus* im L.R.-Verhältnis und im Bau des Hypopygs deutlich abweichend. L.R. beträgt bei den zwei vorliegenden ♂♂ nur 0,63, bei 7 ♂♂ von *caudatus* 0,76—0,81 (Med. 0,79), was einen grossen, schon mit Augenmass feststellbaren Unterschied bedeutet. Das Hypopyg (Abb. 8) nimmt hinsichtlich der Länge des Coxits und der Grösse des Stylus eine Mittelstellung zwischen *caudatus* (Abb. 7) und *morio* (Abb. 9) ein. Bei *morio* beträgt der hinter dem Stylus befindliche Endteil des Coxits nur etwa die Hälfte, bei *forcipatus* etwa Zweidrittel der Gesamtlänge des Stylus. Bei *caudatus* dagegen ist der Endteil des Coxits deutlich länger als der Stylus. Für das *morio*-Hypopyg sehr charakteristisch ist die dichte, feine Behaarung der äusseren (hinteren) Fläche des Stylus. Diese Behaarung fehlt sowohl bei *forcipatus* wie bei *caudatus*. Im L.R.-Verhältnis stimmt *morio* nahe mit *forcipatus* überein: 0,61—0,70, Med. 0,65 (10 ♂♂ gemessen).

Puppe stark an jene bei *caudatus* erinnernd. Im Bau der Frontalhöcker (Abb. 11) und der grossen ventralen Zipfel des VIII. Abd. Segmentes mit

dieser ganz übereinstimmend. Die vorderen Frontalhöcker sind fast 0,10 mm hoch, während die hinteren eine Höhe von nur 0,03 mm erreichen. Die Häute sind durchgehend hell, also wie bei *morio* gefärbt.

Abweichend gebaut scheinen nur die Thorakalhörner zu sein (Abb. 12 --19). Sie sind nämlich konstant kleiner als bei *caudatus* und erreichen meistens eine Länge von 0,20—0,30 mm. In einem Fall wurde eine Länge von nur 0,08 mm gemessen (Abb. 12). In der Form sind sie erstaunenswert variabel, oft ausgeprägt keulenförmig, in anderen Fällen mehr oder weniger spulenförmig. Vereinzelt kommen sogar Thorakalhörner vor, die ganz wie bei *caudatus* mit kleinen distalen Spitzen ausgerüstet sind (Abb. 16). In solchen Fällen kann nur die Grösse der Thorakalhörner als Unterscheidungsmerkmal gegen *caudatus* verwendet werden.

Die von PAGAST (1947, S. 508) erwähnte und von ihm als wahrscheinliches spezifisches Merkmal aufgefasste Zahl der grossen Lateralborsten des Analsegmentes (bei der Exuvie aus dem Starnberger See) liegt innerhalb der Variationsbreite aller *Protanypus*-Arten.

Protanypus turfaceous KIEFF.

Der Typus dieser kleinen, durch doppelte Styli ausgezeichneten Art, stammt aus einem Hochmoor in Estland (KIEFFER 1925, S. 15). Später habe ich (BRUNDIN 1947, S. 48) einen Fund am Toftasjön in Småland veröffentlicht. Eine erneute Untersuchung des småländischen ♂ hat nun ergeben, dass es sich hier tatsächlich um ein abgeflogenes Exemplar der Podonomine *Lasio-diamesa gracilis* KIEFF., bei der die Flügelmakrotrichien abgefallen sind, handelt. Wahrscheinlich ist dies auch mit dem KIEFFERSchen Typus der Fall! Die Beschreibung spricht kaum gegen eine solche Annahme.

Bestimmungstabelle der ♂♂ der europäischen Protanypus-Arten.

- 1 (2) L.R. der Vorderbeine 0,76—0,81. Der hinter dem Stylus befindliche Teil des Coxits deutlich länger als der Stylus. Die äussere (hintere) Fläche des Stylus ohne feine Behaarung. (Abb. 7). Nordeuropäische Art. *P. caudatus* EDW.
- 2 (1) L.R. der Vorderbeine 0,61—0,70. Der hinter dem Stylus befindliche Teil des Coxits kürzer als der Stylus
- 3 (4) Der hinter dem Stylus befindliche Teil des Coxits $\frac{2}{3}$ der Länge des Stylus erreichend. Die äussere (hintere) Fläche des Stylus ohne feine Behaarung. (Abb. 8). Art des Alpengebietes. *P. forcipatus* (EGG.) BRUND.
- 4 (3) Der hinter dem Stylus befindliche Teil des Coxits nur $\frac{1}{2}$ der Länge des Stylus erreichend. Die äussere (hintere) Fläche des Stylus fein und dicht behaart. (Abb. 9). Nordeuropäisch-sibirische Art. *P. morio* ZETT. (*miriforceps* KIEFF.)

Bestimmungstabelle der Puppen der europäischen Protanypus-Arten.

- 1 (4) Die zwei hinteren (sekundären) Frontalhöcker sehr klein und niedrig (Abb. 11). Das Chagrin der Abd. Segm. sehr schwach entwickelt. Die grossen ventralen (beim ♂ einfachen, beim ♀ doppelten) Zipfel des VIII. Abd. Segm. distal mehr oder weniger zugespitzt. (Abb. 4).

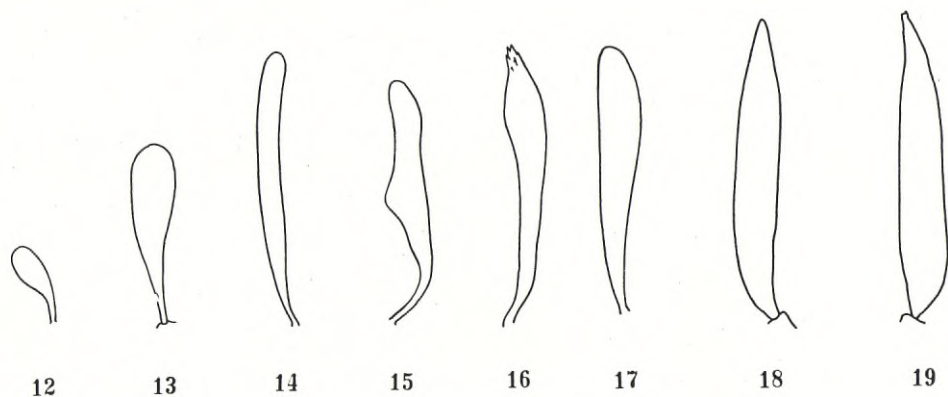


Abb. 12—19. Thorakalhörn der Puppe von *Protanypus forcipatus* aus dem Lunzer Untersee (Abb. 12—18) und aus einem See im Grimselpass, 2 165 m (Abb. 19). Die beiden Thorakalhörner in Abb. 16 und 17 gehören derselben Exuvie an.

- 2 (3) Thorakalhörner länger, 0,45—0,60 mm lang, zylindrisch, distal mit feinen Spitzen. (*P. caudatus* EDW. (Abb. 5, 6).
- 3 (2) Thorakalhörner kürzer, höchstens 0,30 mm lang, keulen- oder spulenförmig, distal nur selten mit feinen Spitzen. (Abb. 12—19). (*P. forcipatus* (EGG.) BRUND.
- 4 (1) Die zwei hinteren Frontalhöcker etwa gleich hoch und kräftig wie die vorderen. (Abb. 10). Das Chagrin der Abd. Segm. kräftiger und gleichmässiger entwickelt. Die grossen ventralen Zipfel des VIII. Abd. Segm. distal breit abgerundet. (Abb. 1). Thorakalhörner gross, 0,60—0,80 mm lang, unregelmässig spulenförmig, distal immer ohne Spitzen. (Abb. 2—3). (*P. morio* ZETT. (*miriforceps* KIEFF.)

Prodiamesa (Monodiamesa) ekmani BRUND.

I m a g o: BRUNDIN 1949, S. 828, Abb. 197, 198.

L a r v e (Abb. 20) der von *Monodiamesa bathyphila* KIEFF. äusserst ähnlich, aber durch folgende Merkmale konstant abweichend: Kopf verhältnismässig kleiner und bei Vertikalansicht schmaler und weniger ausgeprägt dreieckig, Augen erheblich grösser. Das beste Merkmal stellt zweifellos die Augengrösse dar. In den Abb. 20 und 21 sind die Köpfe von zwei gleichgrossen, 11,5 mm langen Larven wiedergegeben. Die Länge der reifen *ekmani*-Larve beträgt 12,5 mm, jene der reifen *bathyphila*-Larve 14—16 mm (THIENEMANN 1944, S. 632).

P u p p e mit der von »*Monodiamesa sp. B*» aus dem Torneträsk und dem Vättern identisch (vgl. die Beschreibung bei THIENEMANN 1941, S. 191, 222—224, Abb. 40).

Mehrere Larven und Puppen liegen mir aus den Seen Stora Blåsjön, Kvarnbergsvattnet, Leipikvattnet und Semningsjön im nördlichen Jämtland vor (leg. A. MÄÄR). Beim Züchten eines im Litoral des Stora Blåsjön gefundenen ♂ wurde die Puppenhaut mit der noch festsitzenden Larvenhaut erhalten. Die spezifische Identität der Larve und Puppe ist demnach sicher festgestellt.

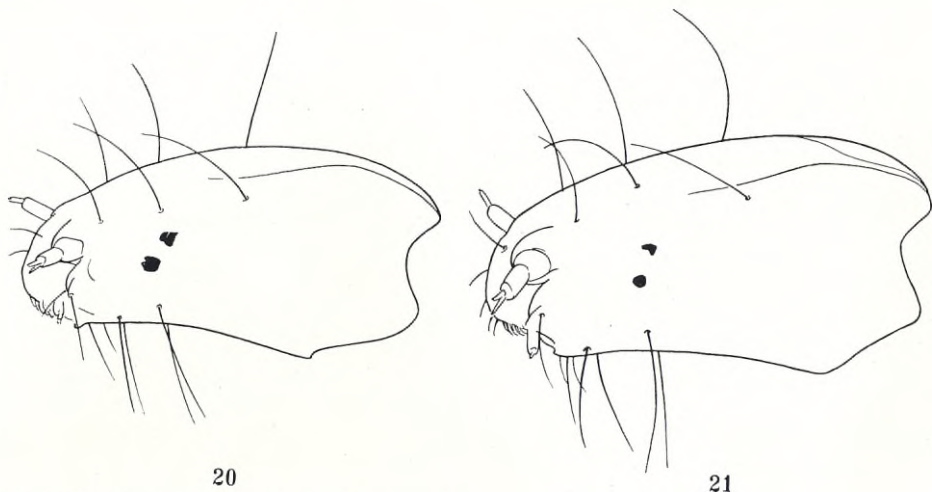


Abb. 20—21. Larvenkopf bei Seitenansicht von *Monodiamesa ekmani* (Abb. 20) und *M. bathyphila* (Abb. 21).

Die von mir (BRUNDIN 1949) unter dem Namen *bathyphila* angeführten Larven und Puppen aus dem Stora Blåsjön, Leipikvattnet und Semningsjön gehören, ebenso wie die nur als *Monodiamesa* bezeichneten Larven aus diesen Seen, tatsächlich alle zu *ekmani*, die also in den subarktischen Seen weit häufiger als *bathyphila* sein muss. Die grösste Tiefe, in der die Larven angetroffen wurden, beträgt 27 m (Stora Blåsjön). Eine Revision meiner småländischen *Monodiamesa*-Larven hat dagegen gezeigt, dass sie in sämtlichen Fällen zu *bathyphila* gehören. Dasselbe gilt für die Larven aus dem Västra Skålsjön in Västmanland (BRUNDIN 1949, Tab. 78, 79).

Die *Monodiamesa*-Larven der skandinavischen Seen vertreten demnach zwei Arten, und es ist dabei wichtig zu bemerken, dass die Larven dieser Arten eine verschiedene ökologische Einstellung haben. Während die *bathyphila*-Larven höchstens als schwach kaltstenotherm bezeichnet werden können, sind die *ekmani*-Larven nach allem zu urteilen ausgeprägt kälteliebend. In Süd- und Mittelschweden sind sie höchstwahrscheinlich nur in den tiefsten und kältesten Seen heimisch. Es dürfte nicht auf Zufälligkeiten zurückzuführen sein, dass *ekmani* in Südschweden bisher nur aus dem Vättern bekannt ist (BRUNDIN l.c., S. 718). Mit Rücksicht auf die verschiedene Ökologie und Verbreitung ist es deshalb eine erfreuliche Tatsache, dass die beiden Arten schon im Larvenstadium trennbar sind.

Prodiamesa (Monodiamesa) alpicola n.sp.

Imago jener von *Monodiamesa ekmani* BRUND. sehr ähnlich und mit ihr in den meisten Merkmalen übereinstimmend. Die wichtigsten Unterschiede liegen im Bau des Hypopygs (Abb. 22, 23), vor allem des unteren Coxit-

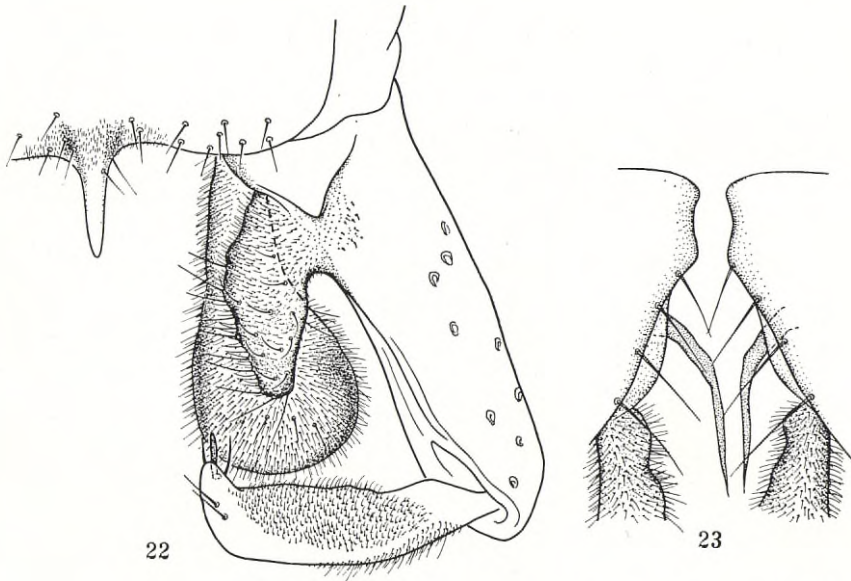


Abb. 22—23. *Prodiamesa (Monodiamesa) alpicola n.sp.* Hypopyg, dorsal (Abb. 22), und Basalpartie der Coxite des Hypopygs mit den ventrobasalen Anhängen und Borsten, Ventralansicht (Abb. 23).

anhangs. Der Stielteil dieses Anhangs ist gerade, kräftiger als bei *ekmani*; der verbreiterte Endteil ist recht regelmässig gerundet und dorsal mit radiär angeordneter Behaarung versehen. Bei *ekmani* ist dagegen der Endteil des Coxitanhangs spatelförmig verbreitert und dorsal mit lateralwärts gerichteter Behaarung versehen. Am Stylus ist die Ansatzpartie des Griffels stärker ausgezogen als bei *ekmani*, etwa wie bei *nitida* (KIEFF.) PAGAST (1947, Abb. 68). Die ventrobasalen, stabförmigen Anhänge des Coxits sind wie bei *ekmani* gebaut. Dagegen scheinen die dorsal davon sitzenden Borsten verschieden angeordnet zu sein (vgl. Abb.). Hervorzuheben ist noch, dass die Vordertarsen bei *alpicola* jede Andeutung eines Bartes entbehren.

Larve der von *bathyphila* sehr ähnlich. Ob konstante Unterschiede tatsächlich vorhanden sind, bleibt noch festzustellen.

Puppe. Der einzige Unterschied gegenüber *ekmani* scheint im Bau der Thorakalhörner zu liegen (Abb. 24, 25). Diese sind bei *alpicola* grösser (Länge 1,4 bzw. 1,1 mm) und basal viel breiter.

Verbreitung. Das mir vorliegende Material stammt aus der Schweiz: Öschinen See, 1578 m, in den Blümlisalpen, 1 ♂ (Typus) 28.8.49 am Ufer (BRUNDIN); Lago Maggiore, 1 ♂ 28.3.47 am Ufer bei Locarno (id.); Briener See, eine Exuvie 24.8.49. (id.). Schon diese Fundorte zeigen, dass die Art im Alpengebiet weit verbreitet ist. Nach den Fangdaten zu urteilen tritt sie in zwei Generationen pro Jahr auf.

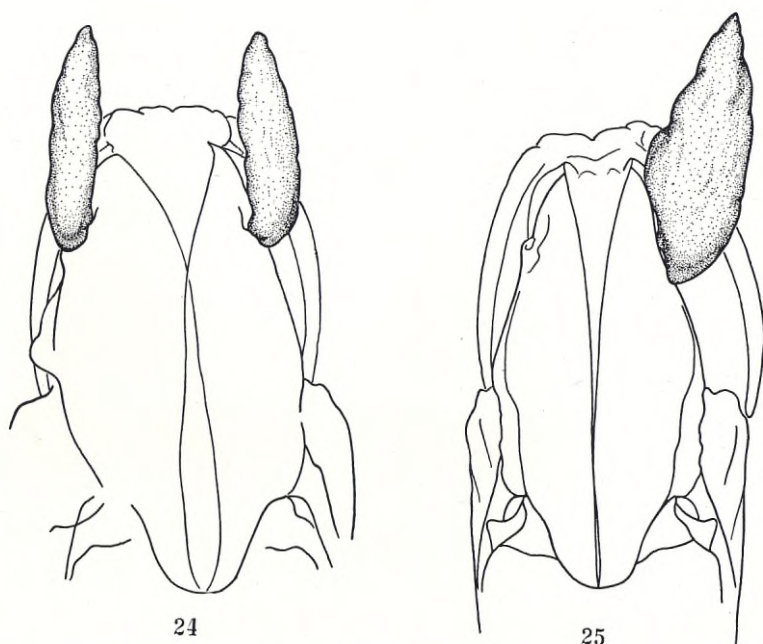


Abb. 24—25. Vorderende der Exuvie, dorsal, von *Monodiamesa ekmani* (Abb. 24) und *M. alpicola* (Abb. 25).

Wahrscheinlich wurde *alpicola* schon vor vielen Jahren an der Südseite der Alpen gefunden. In seiner *Diamesa*-Studie hebt PAGAST (1947, S. 584) hervor, dass ein von MIK am 19.4.1864 bei Görz am Isonzo-Fluss gefundenes ♂ (Mus. Wien) nicht — wie GOETGHEBUER (1932, S. 151) meint — mit *bathyphila* identisch sein kann. Er vermutet stattdessen, dass das Exemplar zu *nitida* (KIEFF.) PAG. gehört. Die von GOETGHEBUER (l.c.) gelieferte Abb. zeigt aber meines Erachtens recht klar, dass wir es hier mit *alpicola* zu tun haben. Die charakteristische Form der unteren Anhänge der Hypopygcoxite muss hier als ausschlaggebend betrachtet werden. GOETGHEBUER's Beschreibung von *bathyphila* (l.c.; 1939, S. 3, Tafelfig. 2) bezieht sich demnach auf *alpicola*.

Prodiamesa (Monodiamesa) bathyphila KIEFF.

Verbreitung. Wie schon oben hervorgehoben, hat sich die Angabe über des Vorkommen von *bathyphila* an der Südseite der Alpen bei Görz (GOETGHEBUER 1932, S. 151) als falsch erwiesen. Wie verhält es sich nun mit den übrigen *bathyphila*-Funden aus dem Alpengebiet? Hinsichtlich des Lunzer Untersees (THIENEMANN 1934, S. 16) hat THIENEMANN (1950, S. 21, Anm. 2) schon mitgeteilt, dass es hier wahrscheinlich von einem Missverständnis einer Angabe bei LENZ (1927, S. 160) die Rede ist. *Monodiamesa*-

Larven sind aus dem Lunzer Untersee bisher überhaupt nicht bekannt. Aus dem Vierwaldstätter See (OBERMAYER 1922, THIENEMANN 1934, S. 16) liegen allerdings Larven vor, aber keine Puppen oder Imagines (THIENEMANN in litt.).

Wir können demnach feststellen, dass keine Belege für das Vorkommen von *bathyphila* in den Alpenseen vorhanden sind. Das von diesen Seen stammende und sicher bestimmbare *Monodiamesa*-Material (Puppen, Imagines) gehört stattdessen zu *alpicola*, die mit der nordischen Art *ekmani* und der bisher nur aus Ungarn bekannten *nitida* am nächsten verwandt ist. Vieles spricht dafür, dass *bathyphila* im Alpengebiet fehlt und dass sie während der Eiszeit eine nördliche Gletscherrandart war.

M. bathyphila ist bisher sicher bekannt aus Fennoskandien, Lettland und zahlreichen Seen in Pommern, Mecklenburg und Holstein (vgl. die Zusammenstellungen bei THIENEMANN 1934, S. 16, PAGAST 1947, S. 585, und BRUNDIN 1949, S. 710). Die Larvenfunde im Lake Windermere in England (HUMPHRIES 1936) und dem Wigry See in Polen (ZAVREL 1926) gehören wohl auch sicher zu *bathyphila*. Ob sich die Funde aus Westsibirien: Nalimje See (PIROZHNIKOV 1933, zitiert nach PAGAST 1947), Japan (TOKUNAGA 1937) und Nordamerika: Green Lake in Wisconsin (JOHANNSEN 1937) wirklich auf diese Art beziehen, muss aber vorläufig als unsicher betrachtet werden.

Über die systematische Stellung der Gattung *Monodiamesa* KIEFF.

In der Beschreibung der *ekmani*-Imago (BRUNDIN 1949, S. 828) habe ich sie in die Gattung *Prodiamesa* KIEFF. gestellt, vor allem deshalb, weil PAGAST in seiner *Diamesa*-Arbeit (1947) die sehr nahe stehende *nitida* KIEFF. als eine *Prodiamesa* aufgefasst und gleichzeitig erklärt hat, dass die systematische Valenz des Begriffes *Monodiamesa* vorläufig unsicher ist. Er hebt hervor, dass ihm von *M. bathyphila* nur eine ♂-Puppe und von »*Prodiamesa*» *nitida* nur zwei trockenpräparierte, weniger gut erhaltene ♂♂ zwecks Untersuchung der imaginalen Merkmale zur Verfügung standen und fügt (l.c., S. 502) hinzu: »Erst Alkoholmaterial beider Arten wird zeigen, ob sie nicht beide zu *Monodiamesa* gehören und wie diese zu *Prodiamesa* steht».

An der Hand der Literatur und des nun vorliegenden Alkoholmaterials der Imagines und Jugendstadien von *bathyphila*, *ekmani* und *alpicola* kann folgendes festgestellt werden:

I m a g i n e s. Bei starker mikroskopischer Vergrößerung tritt klar hervor, dass die Flügel sowohl bei *bathyphila* wie bei *ekmani* mit Mikrotrichien bedeckt sind. Die Angaben bei KIEFFER (1921, S. 287), GOETGHEBUER (1939, S. 2, 3) und BRUNDIN (1947, S. 46), dass die Flügel der zu *Monodiamesa* (mit dem Gattungstypus *bathyphila*) gerechneten Arten keine Mikrotrichien besitzen, sind also nicht stichhaltig. Hierdurch fällt ein wichtiger Unterschied

zwischen *Prodiamesa* (mit dem Gattungstypus *olivacea* MEIG.) und *Monodiamesa* weg.

In seiner Diagnose der Gattung *Prodiamesa* — in der offenbar nur die Arten *olivacea* und *rufovittata* GOETGH. berücksichtigt werden — sagt PAGAST (l.c., S. 496), dass die dorsolaterale Borstenreihe des Mesonotums jederseits durchgehend recht regelmässig zweireihig, hinten manchmal sogar dreireihig ist, und weiter, dass die Supraalarborsten durchgehend auch über der Flügelwurzel einreihig sind und weit nach vorn reichen. Nach meinem Material besitzt das *olivacea*-♂ jederseits etwa 30 Dorsolateralborsten und etwa 15 Supraalarborsten. Beim ♂ von *bathyphila*, *ekmani* und *alpicola* gibt es aber nur 8—10 dorsolaterale und 3—5 supraalare Borsten, die im grossen ganzen einreihig geordnet sind. Beim *bathyphila*-♀ ist die Borstenzahl grösser, und von den etwa 15 dorsolateralen Borsten stehen die hinteren einreihig, während die vorderen eine breite Gruppe bilden. Beim *ekmani*-♀ ist die Chaetotaxis etwa wie bei *bathyphila* entwickelt. Die Chaetotaxis des Mesonotums ist also bei *Prodiamesa* und *Monodiamesa* verschieden entwickelt.

Hinsichtlich *olivacea* ist PAGAST der Meinung, dass das Vorhandensein eines doppelten Stylus am Hypopyg vom phylogenetischen Gesichtspunkt aus keine grössere Bedeutung hat. Hierin stimme ich ihm bei.

Larven. Sowohl *ekmani* wie *nitida* (vgl. THIENEMANN 1941, S. 222, Fussnote) und *alpicola* besitzen Larven des *Monodiamesa bathyphila*-Typus, während die Larve von *olivacea* einen von diesem stark abweichenden Typus vertritt. Interessant ist nun die Tatsache, dass die *rufovittata*-Larve im ganzen jener von *olivacea* recht ähnlich ist (vgl. PAGAST 1933, THIENEMANN 1944).

Puppen. Die Puppen von *bathyphila* einerseits und *ekmani-nitida-alpicola* andererseits sind ziemlich verschieden (die *bathyphila*-Puppe hat einen feinen und kurzen Haarsaum am IV.—VIII. Abd. Segm. und verzweigte Lateralborsten am VII. und VIII. Abd. Segm., THIENEMANN 1918, Abb. 11, 12), unterscheiden sich aber alle von den *olivacea*- und *rufovittata*-Puppen, die einander »recht ähnlich« sind (PAGAST 1947, S. 540), durch das Fehlen der Analborsten im Flossensaum (id., l.c., S. 506—507). Dieser Umstand dürfte bedeutungsvoll sein.

Das vergleichende Studium der fraglichen Arten stützt somit entschieden die Ansicht PAGAST's (1933, 1947), dass die Verwandtschaftsverhältnisse anders liegen, als KIEFFER und GOETGHEBUER vermutet hatten. Die Imaginal- und Jugendstadien zeigen auffallend einstimmig, dass zwei natürliche Artengruppen unterschieden werden können: die *olivacea*-Gruppe (mit *olivacea* und *rufovittata*) und die *bathyphila*-Gruppe (mit *bathyphila*, *nitida*, *ekmani* und *alpicola*).

Nun erhebt sich aber die Frage über den systematischen Rang dieser Artengruppen. Es scheint mir ratsam, auch praktische Dienlichkeitsgründe

walten zu lassen und schlage vor, dass alle Arten wie bei GOETGHEBUER in »Lindner« (1939) in der Gattung *Prodiamesa* vereinigt bleiben, und weiter, dass die *olivacea*-Gruppe und die *bathyphila*-Gruppe in meinem Sinne den Rang als Untergattungen erhalten. Die vom ökologischen Gesichtspunkt wertvolle Name *Monodiamesa* bleibt dadurch immerfort gültig.

Ich gelange demgemäss zur folgenden Gruppierung der fraglichen Arten:

Gattung *Prodiamesa* KIEFF.

Untergattung *Prodiamesa s.str.*

1. *olivacea* (MEIG.)
2. *rufovittata* GOETGH.

Untergattung *Monodiamesa* KIEFF.

3. *bathyphila* KIEFF.
Syn. *nigra* BRUND.
4. *nitida* (KIEFF.) PAG.
5. *ekmani* BRUND.
6. *alpicola* BRUND.
Syn. *bathyphila* GOETGH. (forte).

Bestimmungstabelle der ♂♂ der europäischen *Prodiamesa*-Arten.

(Bemerkung: Die Zahl der Supraalarborsten ist bei *rufovittata* und *nitida* noch nicht sicher festgestellt.)

- 1 (4) Mesonotum mit etwa 15 Supraalarborsten, die weit frontalwärts der Flügelwurzel reichen. Vordertarsen nicht gebartet. Untergattung *Prodiamesa s.str.*
- 2 (3) Hypopyg mit doppeltem Stylus, ohne Analspitze. Die vorletzten Fühlerglieder quer oder (Glied 13) so lang wie breit. Der untere Coxitanhang lang, etwa parallel-seitig. Flügellänge 5 mm. *P. olivacea* (MEIG.)
- 3 (2) Hypopyg mit einfachem Stylus und kräftig entwickelter Analspitze. Der untere Coxitanhang basal sehr schlank, distal rund scheibenförmig verbreitert. Die vorletzten Fühlerglieder länglich. Flügellänge 3,2 mm. *P. rufovittata* GOETGH.
- 4 (1) Mesonotum mit 3—5 Supraalarborsten, die alle in der Nähe der Flügelwurzel sitzen. Analspitze immer vorhanden. Untergattung *Monodiamesa* KIEFF.
- 5 (6) Vordertarsen kräftig gebartet. Unterer Coxitanhang ebenso lang wie der obere, beide fussförmig. A.R.=3. Flügellänge 4,5—5,0 mm. *M. bathyphila* KIEFF.
- 6 (5) Vordertarsen höchstens schwach gebartet. Unterer Coxitanhang viel länger als der obere A.R.=2.
- 7 (8) Unterer Coxitanhang mit kräftiger Basalpartie und fast kreisrunder Distalpartie. Vordertarsen nicht gebartet. Flügellänge 3,3—3,8 mm. *M. alpicola n.sp.*
- 8 (7) Unterer Coxitanhang mit schlanker Basalpartie und länglicher, nach hinten-aussen ausgezogener Distalpartie.
- 9 (10) Vordertarsen schwach aber deutlich gebartet. Die vorletzten Fühlerglieder schwach quer. Flügellänge 3,2—3,5 mm. *M. ekmani* BRUND.
- 10 (9) Vordertarsen nicht gebartet. Die vorletzten Fühlerglieder länglich. Flügellänge 4 mm. *M. nitida* (KIEFF.) PAG.

Zusammenfassung

1. Neues Imagomaterial sowie die bisher unbekanntes Puppen von *Protanypus caudatus* EDW. und *forcipatus* EGG. zeigen, dass diese verschiedene Arten sind. Jene ist eine nordische, arktisch-subarktische, diese eine alpine Form. Zusammen bilden sie ein borealpines Artenpaar.

2. Die bekannte Art *Protanypus morio* ZETT. (*Didiamesa miriforceps* KIEFF.) ist eine nordische Form, die im Alpengebiet zu fehlen scheint.

3. In der »Gattung« *Monodiamesa* werden die Larve von *M. ekmani* BRUND. sowie die Imago und Puppe von *alpicola* n.sp. beschrieben. Jene ist eine nordische, diese eine alpine Art, die in den Seen des Alpengebietes weit verbreitet ist. Auch in diesem Fall scheint es begründet, von einem boreoalpines Artenpaar zu sprechen.

4. Die vorliegenden Tatsachen sprechen bestimmt dafür, dass die bekannte Art *Monodiamesa bathyphila* KIEFF. eine nordeuropäisch-norddeutsche, im Alpengebiet fehlende Art ist.

5. Auf Basis sowohl der Imagines wie der Puppen scheint es gut begründet, *Monodiamesa* nur als Untergattung von *Prodiamesa* zu betrachten. Im Imago-stadium unterscheiden sich diese Untergattungen voneinander nur durch die Zahl und Anordnung der mesonotalen Borsten.

Zitierte Literatur

- BRUNDIN, L. 1947. Zur Kenntnis der schwedischen Chironomiden. *Ark. f. Zool.* 39 A, 3: 1—95.
- 1949. Chironomiden und andere Bodentiere der südschwedischen Urgebirgsseen. *Rept. Inst. Freshwater. Res. Drottningholm.* 30: 1—914.
- EDWARDS, F. W. 1924. A note on the genus *Protanypus* KIEFFER. *Ann. Biol. lacustre*, 13: 119—122.
- EGGER, J. 1863. Dipterologische Beiträge. *Verh. zool.-bot. Ges. Wien*, 13: 1101—1110.
- GOETGHEBUER, M., 1932. Diptères *Chironomidae*. IV. (*Orthoclaadiinae*, *Corynoneurinae*, *Clunioninae*, *Diamesinae*). *Faune de France*, 23: 1—204.
- 1939. *Tendipedidae* (*Chironomidae*). c) Subfamiliae *Diamesinae*. A. Die Imagines. In: LINDNER, *Die Fliegen der paläarktischen Region*, 13 d: 1—28.
- JOHANNSEN, O. A. 1937. Aquatic Nematoceros *Diptera*. Part III, *Chironomidae*: Subfamilies *Tanypodinae*, *Diamesinae*, and *Orthoclaadiinae*. *Cornell Univ. Agr. Exp. Stat. Memoir* 205.
- KIEFFER, J.J. 1921. Diagnoses de nouveaux genres et espèces de Chironomides. *Bull. Soc. Ent. France* 1921: 287—289.
- 1925. Description de deux Chironomides remarquables d'Esthonie. *Bull. Soc. Ent. France* 1925: 15—16.
- LENZ, F. 1925. *Didiamesa miriforceps* KIEFF. Eine neue Chironomide aus der Tiefe der Binnenseen. *Neue Beitr. zur syst. Insektenbiol.* 3, 10: 85—94.
- 1927. Chironomiden aus norwegischen Hochgebirgsseen. *Nyt Mag. f. Naturvid.* 66: 111—192.
- OBERMAYER, 1922. Beiträge zur Kenntnis der Litoralfauna des Vierwaldstätter Sees. *Zeitschr. f. Hydrol.* 2: 3—105.
- PAGAST, F. 1933. Chironomidenstudien. *Stett. Ent. Zeit.* 94: 286—300.

- 1947. Systematik und Verbreitung der um die Gattung *Diamesa* gruppierten Chironomiden. *Arch. f. Hydrobiol.* 41: 435—596.
- THIENEMANN, A. 1918. Untersuchungen über die Beziehungen zwischen dem Sauerstoffgehalt des Wassers und der Zusammensetzung der Fauna in norddeutschen Seen. Zweite Mitteilung. *Prodiamesa bathyphila* KIEFF., eine Chironomide aus der Tiefe norddeutscher Seen. *Zeitschr. wiss. Insektenbiol.* 14: 209—217.
- 1934. Chironomiden-Metamorphosen. VII. Die *Diamesa*-Gruppe. *Stett. Ent. Zeit.* 95: 3—23.
- 1941. Lappländische Chironomiden und ihre Wohngewässer. *Arch. f. Hydrobiol. Suppl.* 17: 1—253.
- 1944. Bestimmungstabellen für die bis jetzt bekannten Larven und Puppen der Orthocladiniinen. *Arch. f. Hydrobiol.* 39: 551—664.
- 1949. Lunzer Chironomiden. Ergebnisse von Untersuchungen der stehenden Gewässer des Lunzer Seengebietes (Niederdonau). *Arch. f. Hydrobiol. Suppl.* 18: 1—202.
- 1950. Verbreitungsgeschichte der Süßwassertierwelt Europas. *Die Binnengewässer* 18: 1—809. Stuttgart.
- TOKUNAGA, M. 1937. *Chironomidae* from Japan. 9. *Tanypodinae* and *Diamesinae*. *Philipp. Journ. Sci.* 62: 21—65.
- ZAVREL, J. 1926. Chironomiden aus Wigry-See. *Arch. d'Hydrobiol. et d'Ichtyol.* 1: 195—220.

Accessories for the determination of dissolved oxygen

By LEIF BRUNEAU

The determination of dissolved oxygen by the WINKLER method is one of the most frequently used determinations in fresh and sea water analysis. Hundreds of authors have, therefore, proposed modifications, especially in reagents, but mostly the method used today is in very close agreement with the original WINKLER prescription. It really seems impossible to simplify the chemical part of the method, and the accuracy of the determination is sufficient in most cases.

In handling thousands of samples for oxygen determination during the past ten years, the author has made several experiments to simplify the routine work from sampling to titration. The experiments have resulted in two new accessories, namely special pipets for the WINKLER reagents and a funnel with a rinsing arrangement for transference of the solution from sample bottle to titration beaker.

The pipets for WINKLER reagents are constructed with three bulbs (Fig. 1). The upper bulb has a volume of about 4 ml and effectively prevents the sucking of reagents into the mouth. Especially when sampling on board it is easy to get the lower part of the pipet over reagent level while sucking. With an ordinary pipet reagent will be sucked up in the mouth in this case, but with this pipet, suggested by the author, the reagent cannot come any further than to the bulb. The pipet has a capacity of 1+1 ml and two parallel samples can, therefore, get their reagent immediately after each other. The pipet mouths must be reduced individually for the two reagents, so as to give the same and proper time of outflow for both of them.

When the solution is transferred from the sample bottle to titration beaker, the bottle and stopper must be rinsed with distilled water in order to get the sample transferred quantitatively. This rinsing is usually done with the help of a siphon. With the new siphons made of plastic a few samples



Fig. 1. Pipet with three bulbs.

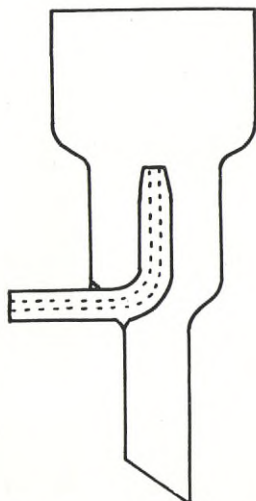


Fig. 2. Rinsing funnel.

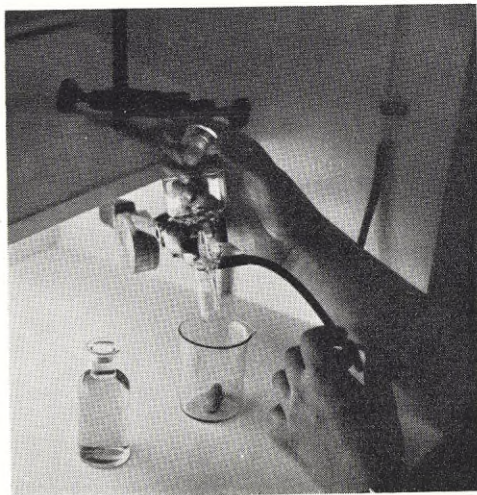


Fig. 3.

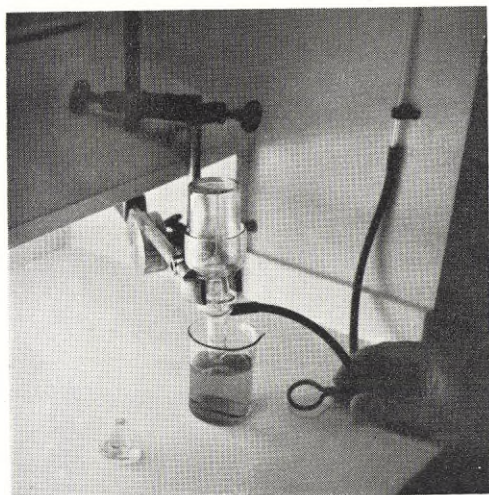


Fig. 4.

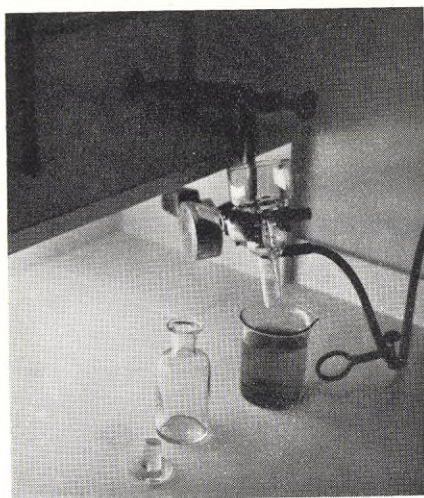


Fig. 5.

Fig. 3—5. The handling of the rinsing funnel. For details see text.

may easily be handled in this way, but when the object is to analyse a series, the author has found the method too tedious. Moreover it is impossible to be sure, that the routine staff really rinses every bottle three times and in such a manner, that the sample will be transferred quantitatively. In order to make the work easier and to reduce the risk of insufficient rinsing, the author constructed a special rinsing funnel (Fig. 2). Usually special bottles of the same size are used for the determination of oxygen. Therefore it is possible to get a funnel suitable for all bottles.

How the funnel should be handled is clearly explained by figures 3 and 4. When the stopper is taken out of the bottle, it is rinsed over the funnel with distilled water from the little jet placed in the centre of the funnel. The bottle with the sample is emptied into the funnel, and the solution flows into the titration beaker. The bottle is then rinsed three times with distilled water from the jet, and the sample is transferred completely. In order to facilitate the removal of the beaker, the funnel may be put at one end of a twoarmed lever. The lever is weighted to make the funnel end lighter than the other. The funnel will therefore rise when not loaded with a bottle, and the beaker is free (Fig. 5). When using erlenmeyer flasks this latter arrangement is not necessary, but in modern titration techniques with a magnetic stirrer, beakers seem to be the most practical and the funnel put on a lever is, therefore, the best solution.

These two accessories have been tested for about six years both ashore and on board by the author and his technicians, and the funnel in particular has been found to simplify the work very much without any reduction in precision. The constructions were included in the preparations for the Swedish Deep-sea Expedition 1947—48 and were used on board by the author.

Salmon Tagging Experiments in Sundsvall Bay of the Baltic in 1950¹

By ARNE LINDROTH

Introduction

The Baltic salmon is caught partly in the rivers and the coastal areas adjoining their mouths, partly in the open sea. The latter fishery, which exploits the salmon when feeding, gives the best yield, a circumstance by which the exploitation of the Baltic salmon stock differs from the fishing on the Atlantic salmon — to which species, *Salmo salar*, L., the Baltic salmon belongs — in the other areas, where this fish is subjected to capture.

During the 1940's the Baltic salmon fishery both on migrating salmon in the salmon rivers and on feeding salmon in the open sea increased very much in yield and attained values, which had not been reached since the end of the last century. The opinion that it is a question of great and possibly regular periodic fluctuations of the total salmon stock of the Baltic seems to be generally accepted (LINDROTH 1950). The present peak period as well as increasing damage done to the reproduction areas of the salmon through hydro electric plants, water impoundments etc. have led to intensified research activities, in Sweden primarily by The Migratory Fish Committee.

The path of the Baltic salmon, when it seeks its way to the spawning rivers, is not known in detail. It is thought that the salmon, which during the river migration season in June—August are caught along the coast with fishing gear close to the shores — bag nets and stake nets (*storryssjor*, *laxkittor* and *nät*) — are as a rule migration salmon. The salmon, which during the greater part of the year are caught with hook and line at varying distances from the coast are thought to be non-migrating fish. How far from the mouth of the home river the migrating fish moves in towards the shore or, to put it another way, how many rivers' stocks of salmon are represented in the shore catch on a certain stretch of coast has, however, scarcely been known.

¹ Report from Bergforsen's Hydro Electric Company.

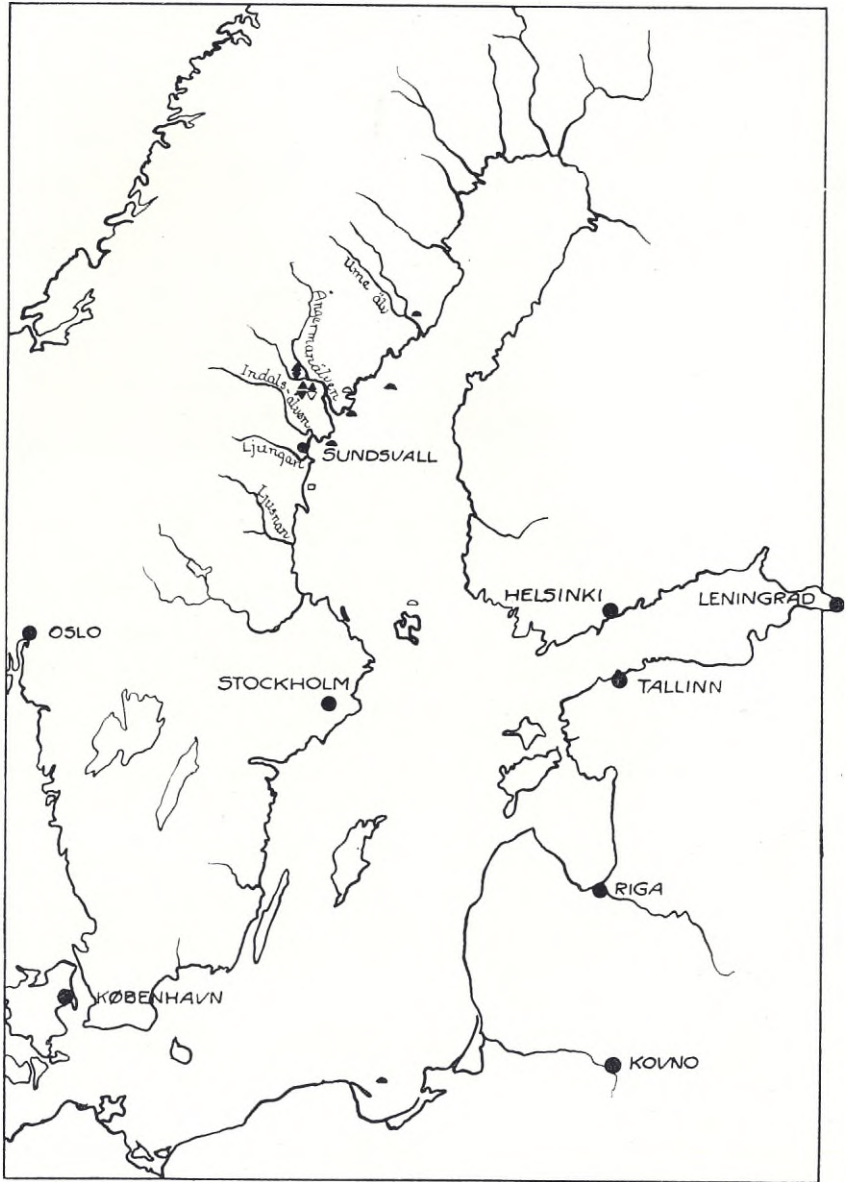


Figure 1. The Baltic and its most important salmon rivers. Recaptures outside the Sundsvall district are indicated; for explanation see Fig. 3. 1 : 10,000,000.

The investigation, of which an account is given here, was made for the purpose of shedding light on the matters in question on a limited section of the coast of the Bothnian Sea, Sundsvall Bay, the area round the mouths of the rivers Ljungån and Indalsälven. (See map, Fig. 1.)

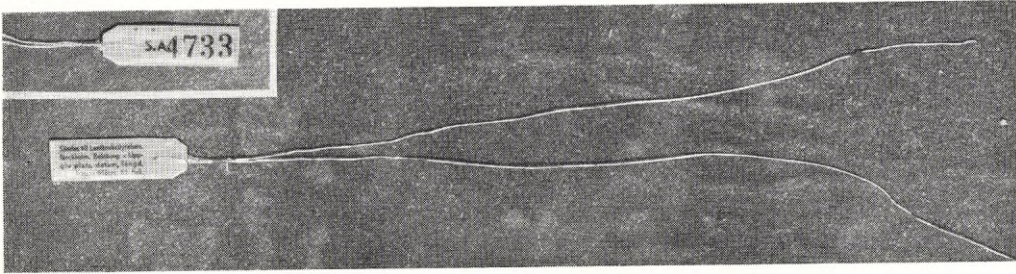


Figure. 2. The tag used. 9 : 10.

Materials and Methods

Altogether 325 salmon were tagged. The tag (Fig. 2) consisted of a piece of cardboard protected by celluloid, $20 \times 7,5$ mm, with number and text fastened by a stainless steel wire to the back at the hind margin of the dorsal fin.

All salmon were caught in bag nets and the release of the tagged fish occurred at the place of capture as soon as possible after measuring length, estimating weight and scale sampling. The fishermen were compensated for the tagged salmon at the current market price.

The tagged salmon varied in size from approx. 40 to approx. 125 cm in length and approx. 1 to approx. 20 kg in weight. 70 of the 325 tagged specimens were stated to be males, 245 females. Scale examination of the tagged material has not yet been carried out.

The situation of the tagging places is apparent from the map (Fig. 3). The number of fish tagged at each place may be found in table 1. The diagram, figure 4, shows the distribution of the tagged salmon during the fishing season.

Altogether 162 salmon have been reported as recaptured, as a rule at commercial fishing (seine nets) in the rivers. During the salmon fishing season numerous advertisements had appeared in the press and in addition to the customary reward, lots were drawn among the tag numbers for cash prizes, amounting to 1,000 *kronor*.

A survey of the distribution of the recaptured fish on the tagging and recapture places is to be found in table 1. The recaptures have been marked on the maps (Fig. 1 and 3).

Results

No tagged salmon were reported as having been recaptured dead.

Three recaptures were made in the open sea (Table 1 Col. 5); one is probably a »feeding fish», which did not spawn the year it was tagged

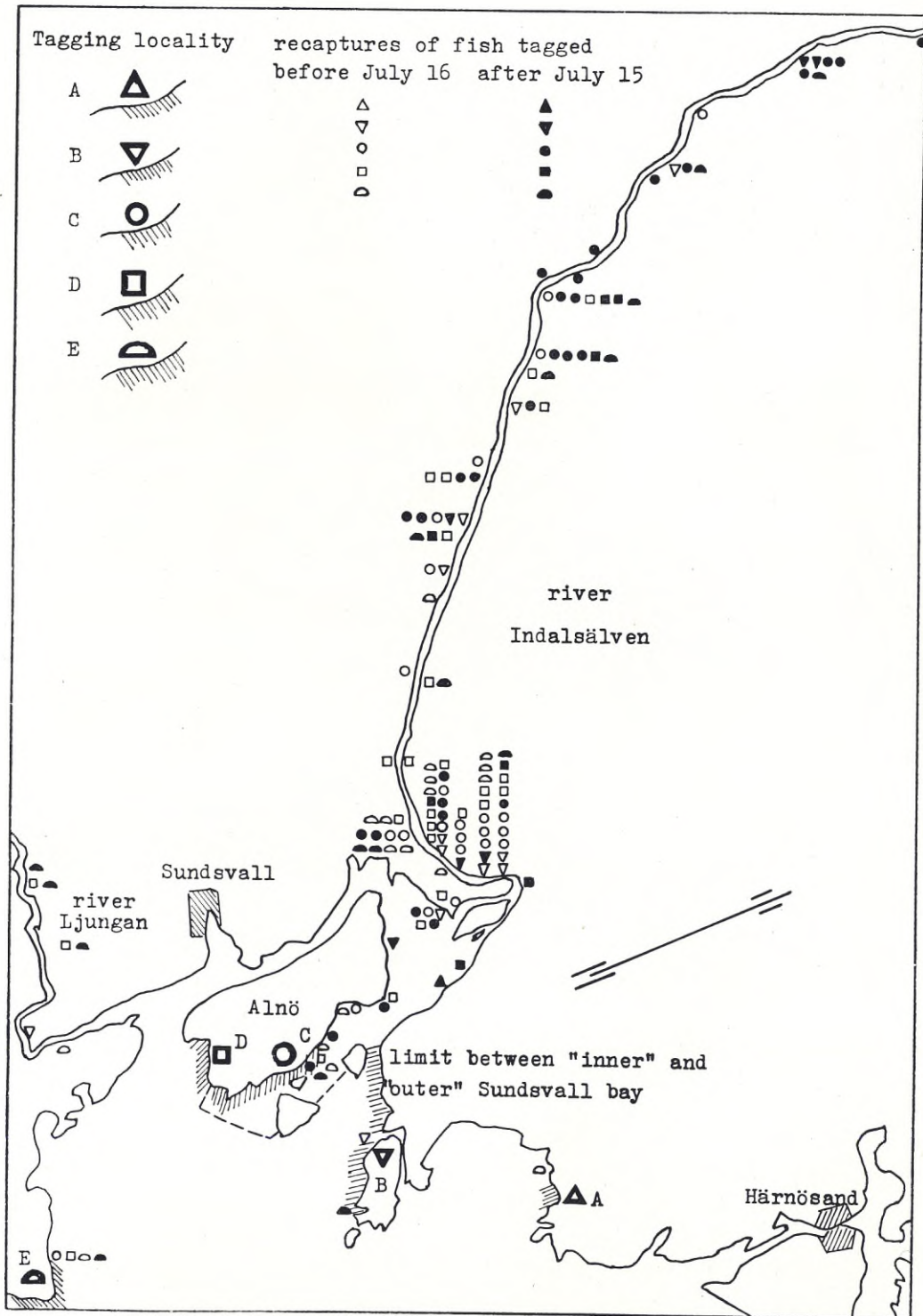


Figure 3. Sundsvall Bay and part of the river Indalsälven with tagging and recapture localities. 1 : 400,000.

Table 1. Tagging of Salmon in Sundsvall Bay during the summer 1950.¹

Tagging		Recapture																			
Locality	Time	Number	Total		A. Bothnian Sea		B. Sundsvall Bay outer	Sundsvall Bay inner		Indalsälven			Ljusnan		The coast		Ångerman-älven		Ume älv		
			Number	% of total tagged (3)	Number	% of total	Number	% of total	Number	% of total	Number	% of total	Number	% of total	Number	% of total	Number	% of total	Number	% of total	Number
1	2	3	4		5	6	7	8	9	8+9	10	11	12	13	14						
A. Åvike	17/7--23/7	17	4	24	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
B. Åkerö-Granön	7/7--1/8	49	22	45	—	1	2	5	10	15	1	—	—	—	—	—	—	—	—	—	—
C. Bjässbodarna- Spikarna	17/6--28/7	98	60	61	—	1	5	12	42	54	—	—	—	—	—	—	—	—	—	—	—
D. Bänkäsviken ...	17/6--28/7	81	36	44	—	1	4	8	20	28	2	6	1	3	—	—	—	—	—	—	—
E. Lörudden- Junibosand ...	3/7--31/7	80	40	48	3	3	4	4	18	22	4	12	—	—	—	—	—	—	—	—	—
Total		325	162	50	3	6	16	29	90	119	78	7	5	1	0.5	3	2	10	4	1	0.5

¹ Addition in proof: during 1952 two further recaptures were reported from the river Indalsälven and one tagged salmon was trapped in the river Ljusnan (*cf.* Fig. 1), indicating a second spawning migration upstreams after an interval of one year in the sea.

(recapture Oct. 2nd), the two others were salmon, which had probably spawned and then returned to the sea (recaptures July 2nd and Dec. 18th 1951).

22 salmon have been recaptured in Sundsvall Bay. Of these 16 have been taken in »inner Sundsvall Bay» (Col. 7), an area which was delimited (see the map) with the aid of the recaptures and in which probably only salmon destined for the Indalsälven were caught. The remaining 6 were caught in »outer Sundsvall Bay» (Col. 6); as far as these are concerned it is not possible to decide whether they belong to the stock of any particular river or even if they belong to the group of two rivers, formed by the Indalsälven and Ljungan.

Regard has neither been paid to the latter category nor to the little group of the three salmon caught in the sea (consequently Col. 5+6), when calculating the percental distribution of the material at different rivers.

In the Indalsälven 119 of the recaptures were made; 29 from these 119 were recaptured on the stretch below Bergefors Bridge, approx. 10 km (Col. 8+9).

From Ljungan 7 salmon were reported, of which 2 were caught in April 1951, probably both on line (which was stated in one case), (Col. 10).

On the coast south of Sundsvall Bay 1 salmon was recaptured in northern Hälsingland, possibly belonging to the salmon stock of the river Ljusnan (Col. 11).

North of Sundsvall Bay 10 salmon have been caught (apart from one of the above-mentioned recaptures in the open sea), of which 3 were on the coast, 6 in the river Ångermanälven and 1 in the river Ume älv (Col. 12—14).

Discussion

Exploitation of migrating salmon

A few experiments of this type have previously been made in Sweden.

In the summer of 1946 39 salmon were tagged at Hertsö salmon fishery at the mouth of the river Lule älv. 16 salmon were later caught in the river, in addition to which one was caught in the archipelago and one was found dead (HULT 1947). It was thought that rather more than 50 % of the salmon travelling up the river were caught with the fishing intensity then prevailing in the Lule älv. The material is, of course, extremely scanty.

The experiments were repeated in the Lule älv in the summer of 1947 (BERG 1948). 99 salmon were tagged and 39 recaptured in the river, in addition to which two were caught in the archipelago and one was captured dead. After correction for the catch in the Hertsö fishery (from which place the release had occurred) the percentage of recaptures was given as 47.

In the summer of 1949 tagging experiments were made from a seine net fishery at Småholmarna in the Indalsälven, approx. 10 km upstream from the mouth of the river (CARLIN 1949). 74 salmon were tagged and 39 re-

captured in the river at and above the tagging place. With due regard to the catch at and below the tagging place it was supposed that rather more than half but probably less than two thirds of the salmon travelling upstream in the Indalsälven were caught before spawning under the prevailing circumstances. It should be noted that after this tagging no recaptures were reported in 1950 but one from the Indalsälven in 1951.

The tagging experiments made in the year 1950 differ from the above-mentioned as the tagging did not take place at the mouth of the river but in the coastal area. The catch risk should, thus, have been greater in the experiment made in the year 1950.

On the other hand the tagging included salmon, which belonged to the stocks of several and partly distant rivers in areas, to which the propaganda for sending in the tags had not been extended (advertising had, however, taken place in the press, which is distributed in the valley of the Ångermanälven). The result of this source of error is the probable reason for the highest percentage of recaptures being reported for the tagging place, whose salmon was solely recaptured in the Indalsälven, the lowest percentage for the tagging place, whose salmon — to judge from the few recaptures — mainly belonged to the more northern rivers.

The average percentage of recaptures is 50. The relative abundance of the material makes it possible to say with some certainty that of the salmon population, which during the migration season 1950 visited Sundsvall Bay, about half or, with regard to the catch at the fishing grounds where tagging had taken place, somewhat more were captured.

Of the 135 recaptured salmon, which could definitely be considered as belonging to the Indalsälven (Col. 7—9), 16 (12 %) were caught on the coast outside the mouth of the river in Klingerfjärden, the remainder or 119 (88 %) in the river itself. This means from a schematic point of view that of the salmon, which intend to travel upstream in the Indalsälven and of which half are caught, about 6 % (or rather more) are captured in Sundsvall Bay before they reach the river, while 44 %, that is to say 47 % of those which pass the mouth of the river, are caught in the river.

Nor is the figure 47 % comparable with the figure, 55 %, CARLIN obtained after the tagging at Småholmarna. A fully comparable figure would be still lower. Agreement is, however, relatively good with regard to the character of the experiments.

The result agrees, as well, with the conclusions reached in the Lule älv experiments. It must be explicitly pointed out, however, that there is no basis for the supposition that the migratory stock of our rivers everywhere and at all times should be exploited to approximately the half. The difference between the fishing intensity in different rivers and during different periods of time, primarily in connection with the great fluctuations of the salmon stocks, must be reflected in varying degrees of exploitation.

The migration to the mouth of the river

If the salmon on its spawning migration in the Baltic approached the coast-line at a greater distance from the home river, the catches in the stationary fishing gears should consist of salmon from several rivers. Out of the recaptures made after the tagging in Sundsvall Bay, which could be assigned to the stock of a particular river (149 specimens, Col. 7—10, 13—14), 95 % have been made in the Ljungan and Indalsälven, 4 % (6 specimens) in the Ångermanälven and 1 % (1 specimen) in the Ume älv. 93 % recaptures in the Indalsälven and Ljungan are obtained for the entire material (153 specimens), if recaptures from the coast are also included (Col. 11—12). Recaptures for tagging place A amounted to 4 specimens, of which 25 % were made in the Indalsälven, the rest in the Ångermanälven. There were 34 recaptures for tagging place E (Col. 7—14), of which 88 % were made in the Indalsälven or Ljungan; at tagging place E all the salmon have been marked, which went north of the Ångermanälven. The coast-line was almost exclusively visited by the salmon, whose spawning river discharges its waters in the immediate neighbourhood; only tagging place E, which constitutes the fishing ground with the most open situation, is passed by salmon which are partly migrating further north.

Tagging experiments with the Atlantic salmon¹ in Norway (DAHL and SØMME), in the British Isles (CALDERWOOD; MENZIES; WENT 1947, 1951) as well as on the east coast of America (BELDING and PREFONTAINE; HUNTSMAN) indicate that migrating salmon tagged on the open coast or in an outer archipelago as a rule distribute themselves over a large coastal area and to several partly distant spawning rivers, while the salmon which have been tagged in an inner archipelago area or at the mouths of the rivers are recaptured in the neighbourhood of the tagging place or in the rivers discharging their waters there. Sundsvall Bay evidently constitutes in the main, in spite of its open situation, an area of the latter type, though with Lörudden (locality E) limiting it to the south as an area of intermediate type.

The salmon in the season of 1950 came into Sundsvall Bay mainly from the south. Past Lörudden (locality E) a salmon stock went by with a slight infusion of strangers and in which salmon from the Ljungan resp. Indalsälven (recaptures in river 4 resp. 26) were included in about the same reciprocal proportion, as the 1950 salmon catch in the two rivers shows. (Indalsälven 8,349 specimens, Ljungan 687 specimens, that is to say 7.5 % in the Ljungan.) After that the salmon divided themselves up between the two rivers; at south Alnön (locality D) Ljungan salmon were still caught but on the east side of Alnön there were salmon from the Indalsälven only. Tynderölandet, the northern limit of Sundsvall Bay, showed beginning participation of salmon from the Ångermanälven.

¹ For sources where no year is stated see MENZIES 1949.

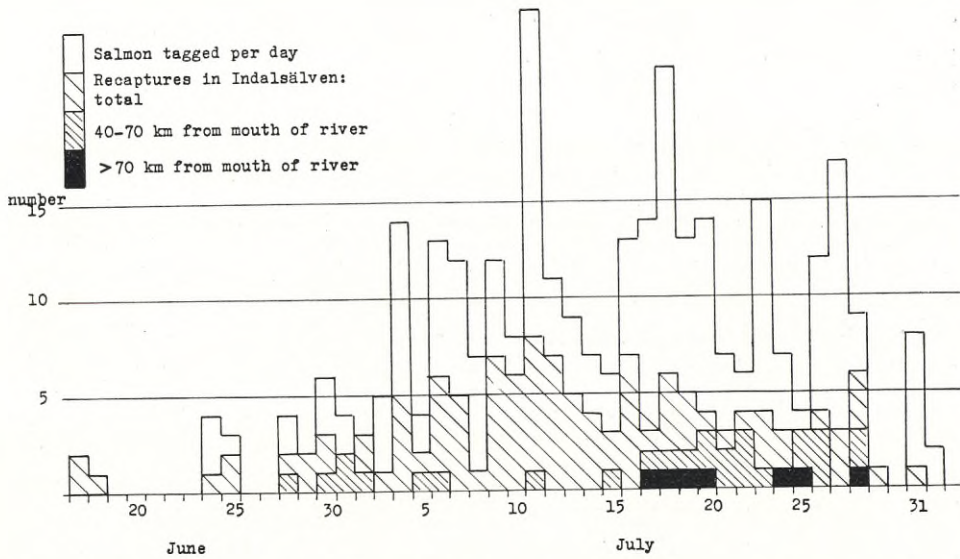


Figure 4. Tagged salmon per day and recaptures in Indalsälven and sections thereof.

The result of the tagging experiment does not contradict the supposition that the salmon on this stretch of coast go in to land first when they come in contact with the water from their home river, whose importance for the homing of salmon is supported by experiments with Pacific salmon and by American experiments on the capacity of fish to discriminate between different kinds of water (HASLER and WISBY 1951). The water from the Ångermanälven should be noticeable with a southbound coastal current as far south as the boundary for the water of the Indalsälven; in accordance with this the greater part of the recaptures (3 out of 4) from tagging place A were made in the Ångermanälven and from tagging place B 3 out of 20. Recaptures from the other tagging places have not been made in the Ångermanälven.

If the reaction on a specific nature of the water leads the salmon towards and up the river, it does not mean that the salmon passively follows the sea currents even after »the spawning migration instinct» has been aroused, until it, at the right time, is carried past the relatively small area, where the concentration of the waters from the home river is strong enough to be detected. It does not seem improbable that some other additional orientation mechanism is engaged, a mechanism whereby the maturing salmon abandons its usual habits and waters as »feeding fish» and is driven to seek out actively the area of the coast, where the home river water can be encountered for further guidance to the spawning area. This conception seems to be supported by tagging experiments with the Atlantic salmon

stock; in the majority of these cases it is unthinkable that passive transport to the area of influence of the home river water is the sole guarantee for the propagation of the salmon in its home river.

The migration in the mouth of the river and up the river

Numerous salmon are caught in the area adjoining the mouths of the rivers in stationary gear laid out there. Although the frequency of this gear can appear to be great in Sundsvall Bay, the depth conditions do not permit the nets to be stretched out far from the shore; they are namely not laid out at a greater depth than approx. 15 m. During its migration through the area adjoining the mouth of the river the salmon does not show any preference for the shallower areas, where it can be caught. Fishermen report that the most abundant catches of salmon are made when weather conditions indicate, that it has probably been driven up to the shallower areas. It thus appears to prefer freer or deeper stretches of water.

The above-mentioned supposition is supported by the tagging results obtained; only 2 of the 325 tagged salmon were caught at the tagging place; of the 98 salmon tagged at locality C, all of which can have been expected to go to the Indalsälven, only 6 (6 %) were caught before they reached the river and of the 177 salmon tagged at localities C and D, practically all of which were destined to the Ljungan or Indalsälven, 12 (7 %) were caught before they reached the rivers.

The salmon, which were recaptured in Sundsvall Bay, 22 specimens, had been at liberty on an average 7.1 days, maximum 27 days.

The salmon, which were recaptured in the Indalsälven below Bergeforsen (approx. 10 km of the river), 29 in number, had been at liberty on an average 7.0 days, maximum 33 days. Thus the salmon does not pass Sundsvall Bay nearly as fast as its swimming speed permits; instead it lingers there for some days. On the other hand there are cases of recaptures in the river as early as the day after tagging; the fastest was a salmon, which after tagging at locality C was caught the following day 16 km up the Indalsälven, 28 km from the tagging place.

The salmon, which were recaptured in the Indalsälven on the stretch 25—40 km from the mouth, a stretch lying above the lower and below the upper spawning areas in the river and which, consequently, should be passed by the salmon on their continued migration upstream, 18 in number, have been caught 12 days after tagging on an average (2—37 days).

The average distance travelled by the three above-mentioned groups was 1.7, 3.6 resp. 4.3 km/d. This difference can be explained either by dissimilarities in the rate of travel in individual fish, a greater danger of capture threatening the slower fish, or — even if all salmon travelled equally fast — by a

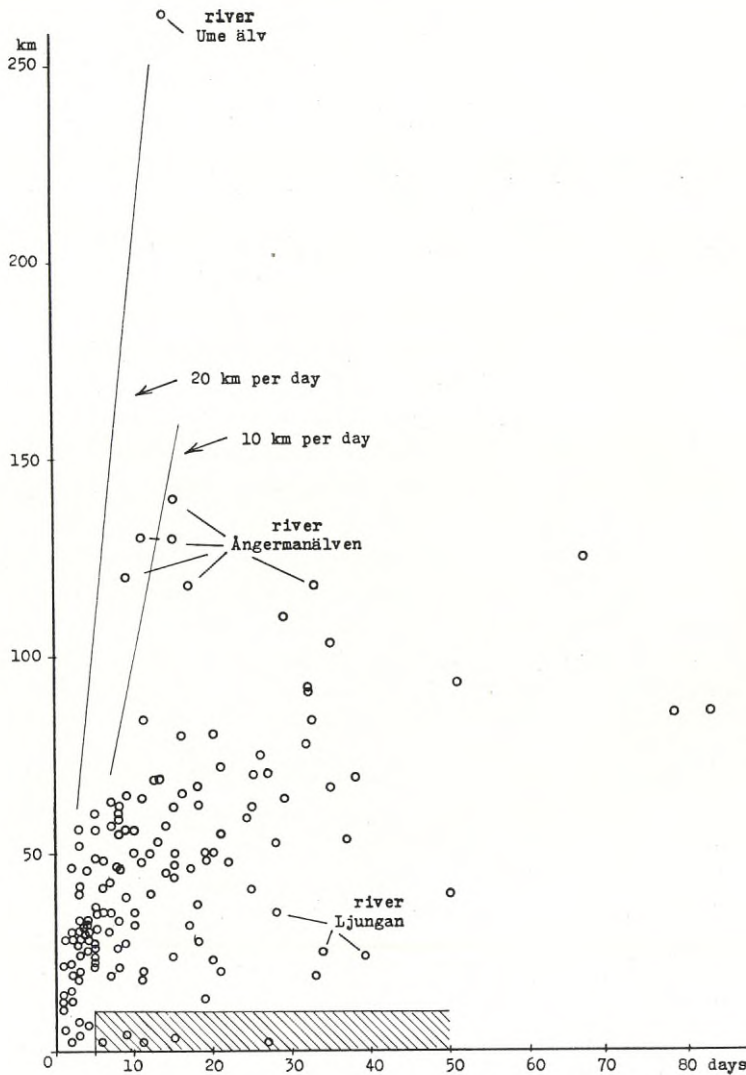


Figure 5. Apparent rate of travel in kilometres per day.

certain amount of time spent in the bay before a more purposeful migration upstream the river takes place. Both explanations are probably applicable.

Rate of travel

The salmon's apparent rate of travel has been already mentioned above. A comparison of the data regarding the recaptures in this respect can be found in figure 5. The data give, of course, not the real swimming speed, because the individual salmon does not swim straight to the place of recapture, and because it can remain a long time there before it is caught.

The fastest salmon was caught, as was stated above, 28 km from the tagging place 1 day later (exact time not given). Mention should also be made of the salmon, which was captured after 14 days at a distance of 265 km (in the Ume älv): an average rate of travel of 19 km/d. Tagging experiments on the Atlantic coasts have given far higher figures for salmon with a longer distance to migrate (MENZIES 1949).

Only 5 salmon have been captured within 10 km from the tagging place after more than 5 days (6, 9, 11, 15 resp. 27 days). In the Lule älv (1946 and 1947) the migration from the tagging place was still quicker, while at the tagging in the mouth of the Indalsälven at Bergforsen (1949) 9 out of 42 salmon were slower and 3 of them were caught after 30—40 days within 5 km from the tagging place, a difference pointed out by CARLIN. This state of affairs can probably be explained by the Lule salmon having already begun their faster river migration (compare previous section) to the spawning areas, all of which are more or less distant, while the Indals salmon have spawning areas approx. 5 km from Bergforsen, in which neighbourhood salmon can quite likely remain during the entire fishing season. An additional factor in the tagging experiments for 1950 is that the tagging took place at the coast and salmon, as has been suggested above, travel more slowly through the area adjoining the mouth of the river.

Time of migration and situation of spawning grounds

The suggestion has been made that at the ascent in the rivers those salmon come first, which have spawning grounds furthest upstream, just as the contrary opinion has been expressed. The present material should be able to shed light on this question.

The diagram fig. 4 shows the distribution in time of the tagged salmon during the fishing season. The diagram should give in the main the frequency of the migratory salmon in Sundsvall Bay in 1950. Recaptures of tagged salmon in the whole of the Indalsälven including »inner Sundsvall Bay» are included in the diagram as well as recaptures in the river at a greater distance than 40 resp. 70 km from the mouth.

Half of the material was tagged before July 15th. The recaptures in the Indalsälven (in an extended sense) of salmon tagged up to and including this day are 78 (48 %), whilst recaptures of salmon tagged later amount to 57 (35 %). This difference is natural, as the salmon tagged earlier are subjected to greater risks of being caught during the limited fishing season.

9 specimens (12 %) of the 78 recaptured salmon tagged before July 15th were caught between 40 and 70 km from the mouth of the river, none higher up. 25 specimens (44 %) of the 57 recaptured salmon tagged later were caught more than 40 km from the mouth of the river and 7 of these (12 %) more than 70 km from the mouth of the river.

The material does not indicate a greater rate of travel in the salmon migrating later. There is, thus, hardly any ground to suppose that there was such a great exploitation of the early migrating fish that they did not get to the more distant spawning grounds. There is no evidence, so far, that the seasonal variation of the average catch-effect of the seine nets in the lower reaches results in such an exploitation.

It seems, thus, to be most probable that the salmon, which come later to the mouth of the river, go further up the river. This state of affairs can be interpreted in that way, that the first salmon to arrive occupy the lower spawning areas, the later ones have to go further. This does not agree very well, however, with the opinion that the homing instinct binds them to a definite spawning area.

Acknowledgements

The investigation was planned in consultation with the Biologist of the Migratory Fish Committee, fil. dr B. CARLIN as well as the Fisheries Inspector of the Lower North District, fil. dr S. BERG and was financed by Bergeforsens Hydro Electric Company.

Summary

In the summer of 1950 325 salmon were tagged in Sundsvall Bay outside the mouths of the Indalsälven and Ljungan. 162 recaptures were later reported, that is to say approx. 50 %. Only a few finds were made outside the above-mentioned rivers. — The salmon catches in fixed gear on the coast in the section in question of the Bothnian Sea obviously consist of salmon belonging to the nearest rivers. — The salmon remain for several days in the bay and then travel more swiftly upstream the river. — It is difficult to state the average rate of travel; it is a matter of approx. 10—20 km/d, but interruptions can delay the migration. — It seems as if the salmon, which come last to the mouth of the river, travel furthest upstream.

Reference

- BERG, S. E. 1948. Unpublished MS.
 CARLIN, B. 1949. Unpublished MS.
 HASLER, A. D. and WISBY, W. J. 1951. Discrimination of stream odors by fishes and its relation to parent stream behavior. *Amer. Naturalist* 85: 223—238.
 HULT, J. 1947. Några resultat av märkning av Luleälvslox sommaren 1946. *Svensk Fiskeri Tidskrift* 1947: 5, 50, 91.
 LINDROTH, A. 1950. Fluctuations of the salmon stock in the rivers of Northern Sweden. *Sv. Vattenkraftfören. Publ.* 415: 98—224. (Swedish with English summary.)
 MENZIES, W. J. M. 1949. The stock of salmon. The Buckland Lectures. London 1—96.
 WENT, A. 1947. Salmon marking in Ireland. *Proc. Roy. Ir. Acad.* 51 B (11): 173—195.
 — 1951. Movements of salmon around Ireland. *Ibid.* 54 B (8): 169—201.

Sur l'écologie du zooplancton Crustacé

Par THOROLF LINDSTRÖM

Table des matières

Introduction	70
Chapitre I: Méthode et instruments de travail	72
Chapitre II: Systématique	74
Chapitre III: Les caractères physico-chimiques de l'eau	76
Chapitre IV: Traitement statistique	79
Répartition aux différentes profondeurs	80
Le cycle annuel	90
Différentes stations d'un même lac	92
Chapitre V: Copépodes: <i>Diaptomus</i>	94
Le cycle annuel	95
La répartition aux différentes profondeurs. La migration diurne	99
Chapitre VI: Copépodes: <i>Cyclops</i>	100
Le cycle annuel	100
La répartition aux différentes profondeurs. La migration diurne	104
Chapitre VII: Cladocères: <i>Daphnia</i> et <i>Bosmina</i>	106
Le cycle annuel des Daphnies	106
Le cycle annuel des Bosmines	107
La répartition aux différentes profondeurs. La migration diurne	107
Chapitre VIII: Autres planctons	110
Zooplancton: Crustacés	110
Zooplancton: Rotifères	111
Phytoplancton	111
Chapitre IX: Le Plancton dans les différentes stations d'un même lac. Différences entre les lacs	112
<i>English summary</i>	113
Index bibliographiques	163

Introduction

Les recherches planctoniques entreprises dans des lacs du Jämtland (Ott-sjön, Hottön, Gesten, Håckren Sällsjön, Ånn) avaient pour but de connaître le degré d'abondance de la nourriture des poissons.

Pour ce faire, on ne pouvait apparemment se contenter d'étudier une série d'épreuves prises un jour au hasard.

A. Il était nécessaire d'examiner si les épreuves prises représentaient bien l'abondance planctonique du moment pour le lac, cela comportait:

1. — une étude des lois qui régissent la répartition des planctons (horizontalement et verticalement)

2. — l'essai de réduire la variation dépendante des facteurs inconnus en prenant les épreuves d'une façon opportune.

B. Il était aussi nécessaire d'étudier les changements dans l'abondance planctonique, changements qui sont soumis à l'alternance des saisons, et les variations de l'abondance planctonique entre des années différentes.

Le but de cette *publication* est de rendre compte des résultats écologiques planctoniques qui se sont révélés dans l'analyse.

Le compte rendu des prémisses est rarement aussi essentiel que pour la publication des recherches planctoniques. Car il est rare que l'on puisse renvoyer le lecteur aux procédés couramment employés et aux points de dépôts généralement acceptés.

En ce qui concerne les méthodes de collecte employées jusqu'à ce jour, on ne peut éviter la source d'erreur qui consiste dans le fait que de grandes formes zooplanctoniques peuvent, grâce à leur propre mouvement, éviter dans une certaine mesure l'engin de capture (VANDEL 1919, VIVIER 1937).

C'est probablement à cause de cette source d'erreur, que les grandes formes zooplanctoniques, pouvant voir le jour l'engin de capture, sont moins nombreuses le jour que la nuit dans les épreuves prises à la même verticale. Cette question n'est pas suffisamment élucidée; pour la discussion, voir SOUTHERN GARDINER (1926, 1932) et RICKER (1938). En dehors de ces erreurs qui n'ont pu être éliminées par la méthode ici employée, il y a d'autres questions de méthode à discuter (voir Chap., I. Méthode et instruments de travail).

La diversité des formes dans les espèces de Cladocères est un fait bien connu. Aussi la diversité des formes chez les espèces de Copépodes a peu à peu attiré l'intérêt des biologistes (voir par exemple: COKER 1934, TONOLLI 1949 a). Dans la première partie du 20ème siècle, WOLTERECK (par ex. 1926, 1928 a) a fait de nombreuses recherches dans le but de découvrir quelles étaient les formes héréditaires et celles dépendantes du milieu. Depuis, les recherches dans ce domaine ont continué mais il y a encore beaucoup à faire.

Il est évident que l'existence dans un même lac de deux espèces ou sous-espèces, qui seraient morphologiquement très semblable est difficile à déceler (par exemple: *Sibling species*). Si on a pensé jusqu'à présent qu'il n'existait qu'un seul type dans un lac, le fait que ces deux types existeraient peut avoir une importance capitale pour la compréhension du cycle annuel et de la répartition dans le sens vertical et horizontal. Pour la discussion, voir Chap. II (Systématique).

Les facteurs qui règlent le cycle annuel des planctons et leur répartition horizontale et verticale sont sûrement nombreux. Le résultat, comportement des planctons dans des lacs différents et à des temps différents est certainement multiforme. L'auteur a dû se limiter et n'a pu rendre compte de tous les nombreux exemples opposés à ses résultats dans les lacs du Jämtland et qui sont cités dans les études planctoniques sur la répartition des planctons.

Quand l'analyse est si compliquée, il est heureux que l'on puisse étudier le comportement des planctons dans des lacs où sont mis hors jeu bien des facteurs qui autrement auraient pu donner lieu à des irrégularités dans la répartition des planctons. Les caractères physiques et chimiques de l'eau, dont on a rendu compte au Chap. III, traduisent un uniformisme qui va loin.

L'application des méthodes statistiques à l'égard des résultats obtenus sur les quantités planctoniques offre certaines difficultés, mais ce qui est pire, il est souvent difficile de savoir quelles hypothèses on doit raisonnablement soumettre à l'application statistique. (Voir Chap. IV.)

I. Méthode et instruments de travail

Trois chercheurs de planctons ont été employés:

1. — En 1946—1947, le chercheur de dix litres décrit par RODHE (1941).
2. — En 1948, un chercheur de 5 litres, de construction un peu différente. Les ressorts métalliques en spiral, manoeuvrant les couvercles étaient remplacés par des ressorts de caoutchouc réunissant les deux couvercles en passant par l'intérieur du chercheur. Cette transformation n'était pas tout à fait satisfaisante, elle augmentait le risque de voir les organismes planctoniques s'attacher au chercheur et ne pas arriver au filtre. Les proportions de ce chercheur étaient presque les mêmes que celles du chercheur de 1950—1951.
3. — En 1950—1951, un chercheur de 5 litres 3, ressemblant davantage, quant au mécanisme de fermeture, à celui décrit par RODHE. Son cylindre de 16 centimètres de diamètre et de 22 cm, 5 de hauteur, le différencie pourtant du chercheur employé en 1946—1947, non seulement par le volume mais aussi par les proportions (Photo).

Les mailles du filtre varient entre 70 et 90 μ .

La méthode employée est source d'erreurs dans les résultats. Aussi, dans l'analyse statistique, sous le terme: »variance intraclasse» est inclus la variation inhérente à la méthode. Afin d'éliminer quelques sources d'erreurs présumées, les séries d'épreuves de 1950—1951, ont été prises en allant de la surface vers le fond du lac. En outre, pour chaque épreuve particulière, le chercheur n'était enfoncé au dernier mètre de profondeur désirée, qu'après estimation que le plomb de sonde était près du chercheur, c'est à dire, que le chercheur se fermait pendant qu'il enfonçait.

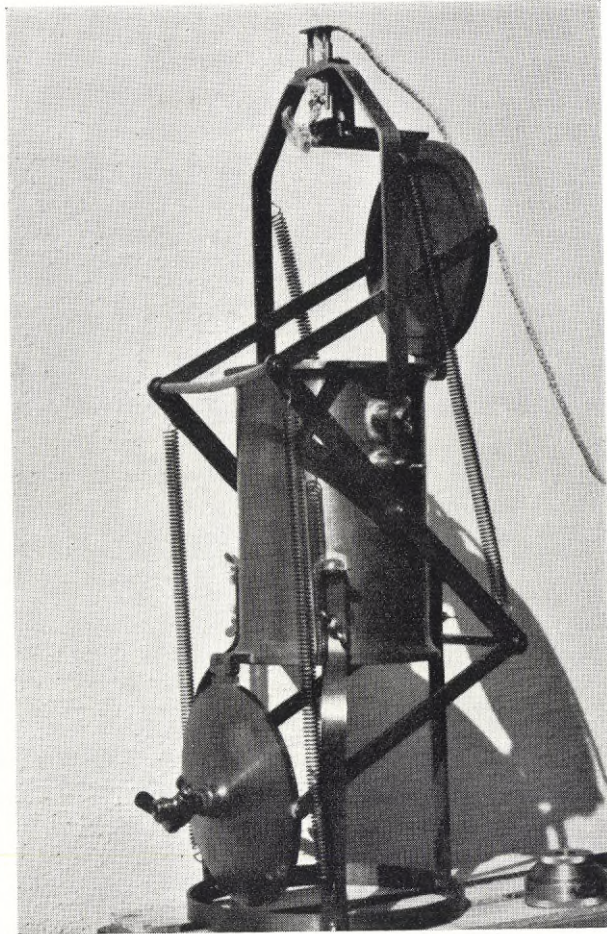


Photo. Le chercheur de plancton employé en 1950 et 1951. L'appareil à filtrer (à droite de la photo) n'était attaché au chercheur que lorsque celui-ci était ramené au bateau après avoir été fermé à la profondeur désirée.

The plankton sampler used 1950—51. The filter supplement (right) is not fixed to the sampler until after the shutter mechanism is released at the desired depth and after the sampler is drawn out of the water.

Pour chaque station, c'est dans un cercle d'une dizaine de mètres que les épreuves étaient prises en évoluant volontairement à l'intérieur du cercle et non pas en restant à un point fixe de ce cercle, car les migrations diurnes des planctons ne sont pas limitées strictement au sens vertical (TONOLLI 1949 c) et les épreuves prises exactement à la même verticale n'ont pas spécialement de point commun entre elles, en regard de l'abondance du plancton. En déplaçant le bateau pour prendre les différentes épreuves dans une même station on peut éviter de donner l'alarme aux organismes qui seront captés dans ces épreuves.

Pour faire l'examen de la méthode, le chercheur était rempli d'une eau dépourvue de planctons, puis, un nombre connu des différentes formes planctoniques y étaient ajoutés. L'épreuve était ensuite traitée comme à l'ordinaire. L'expérience se répétait cinq fois. Les pertes étaient limitées mais l'expérience fut abandonnée car on peut élever des objections quant

à la validité de cette façon d'analyser la méthode. Les travaux de laboratoire, manipulations des épreuves prises, ont été soumis aussi à l'examen de la méthode.

Chaque année des épreuves ont été prises avec un filet à mailles de 70—80 μ (quelquefois un filet à mailles de 150—200 μ).

La température est constatée avec des chercheurs de RUTTNER de 0 lit., 5, munis de thermomètres gradués en centigrades indivis. Les thermomètres étaient de même qualité; ceux employés en 1950 et 1951 ont été comparés par l'auteur avec un thermomètre de précision; l'erreur était de moins d'un demi centigrade. Les valeurs de 1950 et 1951 sont naturellement corrigées.

II. Systématique

Les Daphnies sont sans peigne sur la griffe terminale de leur postabdomen, mais ont un ocelle; elles sont *Daphnia longispina*, O. F. MÜLLER. Vers le point culminant de l'été, toutes les Daphnies ont une épine à la carène, par conséquent on doit classer les Daphnies dans les *Daphnia longispina hyalina*, LEYDIG.

Les Bosmines sont nommées *Bosmina coregoni*, BAIRD (au sens le plus étendu) en conformité avec la classification de BURCKHARDT (1941).

AURICH (1934) parle de *Bosmina longirostris*, *B. coregoni* et *B. fatalis*, comme de trois »*Rassenkreise*», citant l'absence de formes intermédiaires comme signe de distinction entre les *Rassenkreise*. On pourrait faire la même analyse pour les autres Cladocères et Copépodes, mais la situation est compliquée. On trouve souvent dans un lac des formes différentes pour une même espèce. Il peut s'agir alors de formes d'âge différent ou de grandeur différente (problème d'alométrie), ou de modifications influencées par la température ou par d'autres facteurs relevant du milieu, ou encore de différences héréditaires représentant les possibilités de variation à l'intérieur d'une population (voir COKER 1934). Il est aussi possible de penser qu'il existe dans un lac, à l'intérieur d'une même espèce de Cladocères, plusieurs sous-espèces. (Concepts espèces et sous-espèces employés ici sont un peu impropres, voir travail important de Banta 1939.) Quoiqu'il y paraisse, cela n'est pas contradictoire aux travaux évolutionnistes modernes (MAYR 1949), car il faut se rappeler que dans plusieurs lacs de l'Europe centrale, les mâles des Bosmines et des Daphnies sont rares et par conséquent la propagation sexuelle peu fréquente. Aussi la variation des formes des Cladocères de différents lieux y est spécialement marquée, dépendante de la rareté de la propagation sexuelle et des oeufs durables, c'est à dire de l'isolement (voir BURCKHARDT, 1899, p. 680—683, EKMAN, 1922, p. 490).

Dans les lacs du Jämtland les Cladocères, les Diaptomus et les Hétérocopes passent l'hiver comme oeufs durables issus de propagation sexuelle. Il est difficile d'imaginer un mécanisme qui puisse isoler dans ces lacs les sous-espèces l'une de l'autre. La répartition des Crustacés planctoniques est rarement une répartition absolue. Il y a presque toujours des individus qui paraissent à des temps ou à des lieux atypiques pour la grande masse des individus. En outre, les formes sexuelles paraissent en partie pendant l'automne quand la circulation totale doit supprimer l'isolement. Dans les lacs Ottsjön, Gesten et dans la partie étudiée de Ånn, l'isolement ne doit pas pouvoir se produire, même en été, à cause du vent ou de leur grand débit qui mêlent les différentes couches d'eau. Ceci se reflète dans les courbes de température. En conséquence, des sous-espèces différentes à l'intérieur d'une même espèce, ne doivent pas exister dans un même lac de la région actuelle du Jämtland, mais il est possible naturellement qu'il existe des *Sibling species*. Les mêmes conclusions sont valides pour une série de lacs alignés sur le cours du même bassin fluvial, les oeufs durables ayant la possibilité d'y être facilement éparpillés.

Tous les Diaptomus sont *Diaptomus laticeps*, SARS, sauf deux spécimens de *Diaptomus denticornus*, WIERZEJSKI, trouvés dans Ånn.

Les Hétérocopes sont *Heterocope saliens*, LILLJEBORG.

Tous les Cyclopes femelles portant des oeufs ou des spermatophores, sont *Cyclops scutifer*, SARS.

Les copépodites âgés de *Diaptomus* et d'*Heterocope* sont faciles à classer, mais les copépodites très jeunes de ce genre peuvent être confondus par l'auteur.

Dans la classification des Cyclopes copépodites, les jeunes s'entendent du 1^{er} stade au 3^{ème} et même en partie au 4^{ème} stade; les âgés s'entendent en partie du 4^{ème} jusqu'au 5^{ème} inclusivement.

Les nauplii et metanauplii sont classifiés parmi les *Centropagidae* et les *Cyclopidae*, d'après DIETRICH (1915). Dans le mot «nauplii» l'auteur inclu: nauplii *sensu stricto* et metanauplii.

Finalement le matériel de 1948—1951 fut révisé en 1951—1952. Pour le matériel de 1946—1947 on a gardé les épreuves prises avec des filets mais on a rejeté les épreuves prises avec le chercheur. En conséquence, il n'est pas possible d'affirmer que dans les renseignements préliminaires tous les Cyclopes «non-classifiés» de 1946—1947, sans exception, étaient des copépodites âgés, quoiqu'ils en formaient presque la totalité. Des individus isolés pourraient être des femelles adultes sans oeufs, appartenant à d'autres espèces. Comme il a déjà été dit, en dehors des *Cyclops scutifer*, aucun Cyclope adulte femelle, portant des oeufs ou des spermatophores, n'a été attrapé dans ces lacs.

III. Les caractères physico-chimiques des lacs où eurent lieu les investigations

Evaluation de quelques caractères physico-chimiques pour servir à caractériser le milieu où vivent les organismes planctoniques. Des faits sur Hottön et Ånn — ainsi que sur leur plancton — sont donnés dans les travaux de BRUNDIN (1942) et THOMASSON (1951).

La situation et l'altitude des lacs doivent ressortir de la carte 1. Les cartes 3—6 montrent la topographie du fond de quelques lacs. Celle de Ottsjön est faite avec une sonde à ultra-sons, les autres sont faites par simples sondages. Dans les cartes, la situation des stations des épreuves est aussi marquée, ainsi que quelques valeurs du débit et du niveau dans les graphiques 1—2.

Les graphiques 3—14 et les tableaux 1—8 montrent: la température, la transparence, le vent, la teneur en oxygène dissous, la conductibilité, le pH, l'alcalinité, la dureté totale et la teneur en matières organiques. D'autres observations de température peuvent être consultées au Sötvattenslaboriet de Drottningholm, où elles sont conservées.

Rappelons que la région des lacs étudiés est située si loin vers le nord que le soleil ne se couche qu'aux environs de 22 h., le 24 juin; aux environs de 20 h., 50 au début d'août et aux environs de 19 h. à la fin d'août.

Ci-dessous suivent quelques renseignements sur la teneur en phosphore et en azote.

Phosphore total. — Les épreuves sont d'un litre et conservées avec $\frac{1}{2}$ cc CHCl_3 . Elles n'ont pas été filtrées. La méthode de dosage est celle de DENIGÉS et ATKINS, connue de l'auteur par le travail de LOHAMMAR (1938). Contrairement à LOHAMMAR la colorimétrie est faite 20 minutes après avoir ajouté le SnCl_2 en employant un *Zeiss Pulfrich Photometer* à filtre 8, S 72.

Lacs	Dates	γ (1/1000 mg) P par litre d'eau:			Profondeur totale
		Surface		Près du fond	
Sällsjön	21.8.46		22.6	—	17
Gesten	23.8.46		10.3	12	21
Hottön	21.7.47	7	17	6	46—50
	22.8.46		14	—	45

Azote total. — Les épreuves sont d'un litre environ et conservées selon la méthode de LOHAMMAR (1938) avec 1 cc 10 % HCl. La méthode de dosage est celle dont LOHAMMAR a rendu-compte mais la colorimétrie est faite avec un *Zeiss Pulfrich Photometer* à filtre 1, S 43. Une courbe comparatrice correcte était difficile à obtenir pour l'intervalle actuel car les valeurs obtenues par les solutions de NH_4Cl n'entrent pas dans une ligne assez bien définie. Il ne faut donc pas attacher trop de signification aux valeurs de la teneur exacte en azote. Cependant les valeurs doivent indiquer

grossièrement la teneur de l'eau en azote. Des 8 valeurs calculées pour N total par 100 cc d'eau, exprimées en γ (1/1000 mg), 5 valeurs se situent entre 9 γ et 11 γ . La valeur la plus élevée est 15 γ , la plus basse, au dessous de 5 γ . Les épreuves sont prises dans Sällsjön le 21.8.46, dans Gesten le 23.8.46, dans Hottön le 22.8.46. et dans Ottsjön le 17.8.46. Pour chaque lac il y a une épreuve près de la surface et une autre près du fond.

Les valeurs des propriétés physico-chimiques de l'eau ne seront pas employées pour une discussion limnologique de la production. L'auteur veut seulement dire en passant que les valeurs de conductibilité et la teneur en azote et en phosphore tombent ordinairement au dessous des valeurs modales pour les séries des lacs du nord de la Suède dont LOHAMMAR a rendu-compte (1938). Il est intéressant aussi de noter que les valeurs de dureté, d'alcalinité et de conductibilité vont bien avec les *standard curves* et *standard composition* pour le type bicarbonate des lacs discutés par RODHE (1949).

Le but principal de la publication de ces tableaux et graphiques des propriétés physico-chimiques est d'illustrer l'uniformisme dans ces lacs. La signification de cet uniformisme est déjà soulignée dans l'introduction. Cependant on peut noter quelques différences entre l'eau des différentes régions.

Hottön est stratifié thermiquement. Dans Håckren on peut observer un thermocline immédiatement au dessus du fond — l'hypolimnium manque. Dans Gesten le plus grand fond montre de temps en temps une température plus basse que celle de la grande masse d'eau du lac.

Un coup d'oeil sur les courbes de température montre combien Ottsjön est exposé aux vents, chose probablement en partie limitée localement, en partie dépendante du climat généralement très venteux de la région des hautes montagnes. Sur les courbes de température on peut voir que si les eaux de surface étaient plus chaudes que les eaux profondes après quelques jours de calme et de soleil, les courbes devenaient bientôt droites, démontrant l'effet du vent des quelques jours venteux, sur la température de l'eau.

Des différences de conductibilité entre les couches près de la surface et celles près du fond sont évidentes dans Hottön, les valeurs des épreuves prises près du fond étant les plus fortes. Ce lac est stratifié thermiquement. Ces différences sont aussi relevées, plus faiblement il est vrai, pour Ottsjön, à certains jours mais ne sont pas relevées dans ce lac à d'autres jours. La divergence entre Hottön et Ottsjön concorde avec l'absence de stratification thermique dans Ottsjön.

La station X dans Ottsjön montre d'autres caractères spéciaux. C'est une crique protégée, peu profonde et avec des végétaux littoraux bien développés

en comparaison avec les autres endroits de Ottsjön. On peut comparer les valeurs obtenues dans la station X avec celles obtenues dans la station T, située dans le plus grand affluent, à la date du 21.8.50. La teneur en oxygène est plus basse dans X, le pH plus élevé, l'alcalinité beaucoup plus haute ainsi que la teneur en matières organiques. Il faut aussi noter que l'alcalinité, le pH et la teneur en matières organiques sont extrêmement élevés comparés avec toutes les autres valeurs des tableaux, alors que dans la station T la teneur en matières organiques est au contraire extrêmement basse.

Suivent quelques commentaires de moindre importance sur les tableaux. Les valeurs du tableau 1 montrent des changements annuels dans la transparence. La transparence est souvent la plus basse au printemps quand l'eau se trouble sous l'action érosive des crues printanières des ruisseaux et des fleuves à la fonte des neiges. L'eau peut aussi être troublée occasionnellement pendant l'été (voir Gesten le 1.8.51). Le trouble peut aussi être l'effet d'un vent fort sur l'eau d'un lac à régions très peu profondes et très étendues, du fait que le fond vaseux est agité (Ånn 6.6.46). Le caractère spécial d'Ånn est aussi discuté ci-dessous.

Les épreuves de Gevsjön 14.5.47 et de Ottsjön 28.5.50 indiquent que la variation de conductibilité est petite entre des épreuves prises au même temps et au même lieu. Les épreuves d'octobre 1946 prises à l'époque de la circulation automnale dans les deux lacs géographiquement proches, Hottön et Gesten, montrent aussi deux valeurs très rapprochées. L'instrument employé est très juste (*Philips Universal measuring bridge*, type GM 4140. Mais peut-être doit on dire que les échantillons ne sont dosés qu'après quelques jours.) Il est donc admissible de chercher à interpréter les résultats comme suit: Les valeurs des épreuves de Ånn et de Gevsjön (bassin fluvial de Åreälven) sont plus élevées que celles du bassin fluvial de Storån (voir carte 1). Il est possible que les électrolytes sont plus souvent amenés de la vase du fond, souvent agitée, dans les régions peu profondes et très étendues de Ånn, par l'action des eaux remuées par le vent. Dans le bassin fluvial de Storån les épreuves prises en hiver montrent les valeurs de conductibilité les plus fortes de toutes les saisons. Il est probable que la grandeur du débit a une influence sur la conductibilité mais qu'une autre influence est prédominante. Le débit dans Ottsjön était grand au printemps, après la fonte des neiges et le 31.7.50, après quelques jours de fortes pluies. OHLE (1940) constate que dans certaines régions d'Abisko, la fonte des neiges et le grand débit du printemps provoquent une dilution de l'eau, c'est à dire que la valeur de conductibilité descend rapidement mais augmente plus tard pendant l'été. Ces observations sont faites dans une région où la terre est riche en calcium. D'autres régions d'Abisko où les eaux sont moins riches en calcium donnent des résultats en partie conformes avec ceux obtenus dans les lacs actuels du Jämtland.

IV. Traitement statistique

Les facteurs qui pourraient régler la répartition et le cycle annuel des planctons sont nombreux. Ces facteurs peuvent influencer sur l'ontogénèse, la propagation, la mortalité ou bien ils peuvent provoquer des migrations. On peut nommer: l'espace, la température, la lumière, les courants, la teneur en oxygène et d'autres facteurs chimiques, l'abondance de nourriture pour les animaux, l'action des animaux, outre les poissons, qui mangent les organismes zooplanctoniques. On peut toujours recueillir une combinaison de facteurs qui peut expliquer les particularités dans un groupe d'épreuves. Mais ce n'est qu'une hypothèse *a posteriori*; peut-être que la première épreuve prise après la parution de ce travail demandera une autre combinaison de facteurs..

Sont acceptées comme des hypothèses *a priori* les hypothèses qui sont traitées dans les renseignements préliminaires (voir plus bas) et une hypothèse concernant l'effet du vent. Il est évident qu'il existe d'autres prémisses pour le traitement statistique par ex: L'existence d'une migration diurne et d'un cycle annuel des planctons — ces phénomènes sont déjà profondément étudiés par d'autres auteurs.

Un brassage des eaux doit amener un uniformisme tel qu'il est démontré dans le chapitre précédant et en même temps, empêcher, plus ou moins efficacement les planctons d'aller trouver les endroits auxquels ils aspirent et amener une répartition uniforme des planctons. Un tel effet est produit, par exemple par la circulation automnale (RUTTNER 1930 p. 83) ou par des vents forts. L'effet des vents forts sur la répartition, spécialement sur des phytoplanctons a été démontré par RUTTNER (1930) et par MACKAY (1951). Pour la région du Jämtland examinée, spécialement en ce qui concerne Ottsjön, les vents ont un effet fortement remuant, même en été. Ce fait donne l'appréciable possibilité de comparer la répartition des planctons, relativement uniforme, par jours venteux, à la répartition par jours calmes, pendant lesquels les planctons ont les plus grandes possibilités d'aller trouver les régions auxquelles ils aspirent.

Si on a relevé l'absence d'une forme dans les échantillons, cette absence ne prouve pas que cette forme n'existe pas dans le lac. Au contraire, des individus isolés paraissent souvent à des temps et à des lieux atypiques.

Lorsque pour certains lacs, les épreuves ne sont pas assez nombreuses pour que l'analyse soit poursuivie efficacement, liberté est laissée aux hypothèses. Pourtant l'auteur veut néanmoins rendre compte de ces lacs dans chap. V—VI pour montrer à quel point la situation est complexe. L'analyse essentielle n'est poursuivie que pour les lacs où les épreuves sont nombreuses.

Si c'est seulement le hasard qui règle la distribution des planctons on doit obtenir une distribution de Poisson quand on compte les planctons des épreuves prises avec le chercheur de plancton. (FREIDENFELT 1925, RICKER 1937, 1938). Le livre de BONNIER TEDIN (1940) a introduit l'auteur dans les méthodes statistiques employées par FISCHER. Suivant BONNIER TEDIN on a supposé que les tables de χ^2 et de quotient de variance sont applicables quand $S(x)$ — ou $n \times \bar{x}$ — dépasse 15.

Répartition aux différentes profondeurs

L'effet du vent. — L'effet du vent est analysé avec les épreuves de jour prises dans Ottsjön (1950). Les épreuves de 1951 sont rarement incluses dans l'analyse.

Si on attend une répartition 1, 1, 1, ou 1, 1, 1, 1, pour les profondeurs qui entraient dans l'analyse, le tableau (p. 81) en donne les valeurs de χ^2 . Dans plusieurs cas on peut additionner les χ^2 et analyser l'hétérogénéité (p. 82). Les écarts d'une répartition 1, 1, 1, ou 1, 1, 1, 1, sont dans presque tous les cas plus grands les jours avec vent faible ou calme. Le χ^2 pour ces écarts par jours calmes ou avec vent faible mérite le signe *** pour les Cyclopes (toutes formes) et pour les Daphnies, le signe ** pour les Bosmines, et le signe * pour les Diaptomus nauplii etc. (Les Diaptomus copépodites ne sont pas assez nombreux pour entrer dans l'analyse des jours calmes). Pour les Diaptomus, les Daphnies et les Bosmines les écarts d'une répartition 1, 1, 1, par jours venteux ne sont pas indiqués avec le matériel; ils ne dépassent pas ceux qui peuvent être provoqués par hasard. Pour les Cyclopes copépodites jeunes et Cyclopes adultes les écarts sont faiblement indiqués et pour les Cyclopes nauplii et copépodites âgés ces écarts méritent le signe *** même les jours venteux. Ces deux dernières formes doivent faire l'objet d'une discussion spéciale.

Le 15.7, les copépodites âgés de *Cyclops* sont rassemblés dans les couches supérieures (épreuves de surface et de 5 m.). Peut-être préfèrent-ils les couches de 2 à 5 m.? Cela ne ressort pas de la répartition des jours calmes qui entrait dans l'analyse ci-dessus, mais d'autres épreuves le donne à penser.

D'où vient que par jour de vent la répartition des *Cyclops* nauplii ne s'accorde pas avec une répartition 1, 1, 1, ou 1, 1, 1, 1? Ces animaux sont donc moins capables que les autres de combattre de leur propre mouvement le brassage produit par le vent. Si l'on se rapporte à l'analyse qui suit, de la répartition par jours calmes, on constate que les nauplii se rassemblent alors dans les couches profondes. S'appuyant sur ce fait on peut comprendre que l'effet du vent n'influence pas aussi fortement la répartition des nauplii. Le plus grand nombre d'entre eux ne sont pas amenés jusqu'aux couches influencées par le brassage. Aussi les jours de vent l'abondance est-elle plus

Formes	Profondeurs	Dates	Vent	χ^2	P entre:
<i>Diaptomus</i> nauplii	Surface, 5, 10 m.	12.5, 26.5, 10.6 (1950)	Fort	1.14	0.7—0.5
	» 5, 10 »	27.5, 15.6 (1950)	Faible ou calme	8.88*	
<i>Diapt. cop.</i>	Surface, 5, 10 m.	12.5, 26.5, 10.6 (1950)	Fort	4.35	0.2—0.1
<i>Diapt.</i> adultes	Surface, 5, 10 m.	10.6 (1950)	Fort	0.29	0.9—0.8
	» 5, 10 »	15.6 »	Faible	4.30	0.2—0.1
	Surface, 2, 5, 10 m.	17.8, 25.8 (1950)	Fort	1.29	0.8—0.7
	» 2, 5, 10 »	11.8, 20.8 (1951)			
» 2, 5, 10 »	26.8 (1950)	Calme	24.15***		
<i>Cyclops</i> nauplii	Surface, 5, 10 m.	12.5 (1950)	Fort	2.47	0.3—0.2
	» 5, 10 »	15.7 »	»	20.71***	
	» 5, 10 »	17.8 »	»	2.57	0.3—0.2
	Surface, 2, 5, 10 m.	» »	»	8.38*	
	Surface, 5, 10 m.	25.8 »	»	7.37*	
	Surface, 2, 5, 10 m.	» »	»	8.11*	
	Surface, 5, 10 m.	4.7 »	Faible	9.50**	
	» 5, 10 »	23.7 »	Calme	25.78***	
	» 5, 10 »	14.8 »	Faible	37.55***	
	» 5, 10 »	26.8 »	Calme	38.46***	
Surface, 2, 5, 10 m.	» »	»	68.21***		
<i>Cyclops</i> cop. jeunes	Surface, 5, 10 m.	12.5 (1950)	Fort	4.24	0.2—0.1
	» 5, 10 »	10.6 »	»	3.02	0.3—0.2
	» 5, 10 »	27.5 »	Calme	17.40***	
	» 5, 10 »	15.6 »	Faible	10.36**	
<i>Cyclops</i> cop. âges	Surface, 5, 10 m.	15.7 (1950)	Fort	27.50***	
	» 5, 10 »	4.7 »	Faible	12.92**	
	» 5, 10 »	23.7 »	Calme	9.30**	
<i>Cyclops</i> adultes	Surface, 5, 10 m.	10.6 (1950)	Fort	0.62	0.8—0.7
	» 5, 10 »	17.8 »	»	2.24	0.5—0.3
	Surface, 2, 5, 10 m.	» »	»	2.29	0.7—0.5
	Surface, 5, 10 m.	25.8 »	»	4.46	0.2—0.1
	Surface, 2, 5, 10 m.	» »	»	2.50	0.5—0.3
	Surface, 5, 10 m.	15.6 »	Faible	12.38**	
	» 5, 10 »	4.7, 23.7 (1950)	Faible — calme	3.65	0.2—0.1
	» 5, 10 »	14.8 (1950)	Faible	5.72	0.1—0.05
	» 5, 10 »	26.8 »	Calme	22.58***	
Surface, 2, 5, 10 m.	» »	»	26.36***		
<i>Daphnia</i>	Surface, 5, 10 m.	10.6, 15.7 (1950)	Fort	0.43	0.9—0.8
	» 5, 10 »	17.8, 25.8 »	»	3.56	0.2—0.1
	Surface, 2, 5, 10 m.	» » »	»	9.39*	
	Surface, 5, 10 m.	15.6, 4.7, 23.7 (1950)	Faible — calme	5.49	0.1—0.05
	» 5, 10 »	14.8, 26.8 (1950)	» — »	23.34***	
Surface, 2, 5, 10 m.	26.8 (1950)	Calme	54.41***		
<i>Bosmina</i>	Surface, 5, 10 m.	12.5, 26.5 (1950)	Fort	4.26	0.2—0.1
	» 5, 10 »	27.5, 15.6 »	Calme — faible	13.06**	

grande à 10 m. qu' à 5 m. et plus grande à 5 m. que dans les épreuves de surface.

Par jour calme:

Les Bosmines évitent la surface.

Les Daphnies évitent la surface et montrent un maximum à 5 m. (2 m.) de profondeur. L'hétérogénéité entre les époques différentes est insignifiante.

	<i>Cyclops nauplii</i>						<i>Cyclops copépodites jeunes</i>					
	Vent fort			Vent faible ou calme			Vent fort			Vent faible ou calme		
	χ^2	Degrés de liberté	P entre	χ^2	Degr. de I.		χ^2	Degr. de I.	P entre	χ^2	Degr. de I.	P entre
Somme des χ^2	33.1***	8		111***	8		7.3	4	0.2—0.1	27.8***	4	
χ^2 pour la somme	21.2***	2		89***	2		6.7*	2		24.4***	2	
χ^2 pour l'hétérogénéité	12.0	6	0.10—0.05	22***	6		0.6	2	0.8—0.7	3.4	2	0.2—0.1

	<i>Cyclops copépodites âgés</i>						<i>Cyclops adultes</i>						<i>Daphnia</i>					
	Vent faible ou calme			Vent fort			Vent faible ou calme			Vent fort			Vent faible ou calme			Vent fort		
	χ^2	Degr. de I.	P entre	χ^2	Degr. de I.		χ^2	Degr. de I.	P entre	χ^2	Degr. de I.	P entre	χ^2	Degr. de I.	P entre	χ^2	Degr. de I.	P entre
Somme des χ^2	22.2***	4		7.3	6	0.3—0.2	44.3***	8		4.0	4	0.5—0.3	28.8***	4				
χ^2 pour la somme ...	20.0***	2		7.0*	2		26.1***	2		3.0	2	0.3—0.2	26.6***	2				
χ^2 pour l'héter. ...	2.2	2	0.5—0.3	1.3	4	0.9—0.8	18.2**	6		1.0	2	0.7—0.5	2.2	2	0.5—0.3			

Les Cyclopes nauplii, copépodites jeunes et âgés et les adultes évitent la surface. L'hétérogénéité entre les différents jours est certainement significative pour les nauplii et les adultes, mais cette hétérogénéité concerne les différences entre les épreuves de 5 m. et de 10 m. et ne concerne pas la pauvreté dans les épreuves près de la surface.

La migration diurne. — Quoique la migration diurne puisse être fort marquée pour certaines espèces, elle n'est jamais un déplacement de tous les individus d'une couche profonde vers une couche supérieure et vice versa. Elle peut plutôt être regardée comme un déplacement du centre et des *quartiles* de la population (voir PENNAK 1944, PLEW PENNAK 1949). Si le matériel ne suffit pas pour une analyse plus complète (*Diaptomus* ci-dessous) on peut pourtant illustrer la migration diurne avec le changement d'abondance dans la couche près de la surface ou dans celle près du fond.

Les jours de vent sont évités autant que possible dans l'analyse de la migration diurne.

L'abondance de *Diaptomus* adultes dans la couche près de la surface, dans Ottsjön est analysée. L'analyse est faite comme si nous avions une division hiérarchique au lieu d'une division collatérale, à cause du nombre irrégulier des variables dans les classes différentes. Les épreuves sont prises dans le bassin central (A—B—C—D). Le matériel est divisé en quatre classes.

	Dates	Partie du jour	Moyenne	Nombre des épreuves
Classe superordonnée:				
Juin-Juillet 1950 ...	15.6, 20.6, 4.7, 23.7 16.6, 4.7, 5.7	midi soir et nuit	2.9 4.3	7 6
Août 1950, 1951 ...	22.8, 26.8 (1950) 11.8, 20.8 (1951) 21.8, 22.8, 26.8, 30.8 (1950) 15.8 (1951)	}midi }soir et nuit	1.6 8.1	16 26

A cause de l'épreuve du 15.6.50 (15 litres), il est nécessaire de donner les quelques valeurs ci-dessous comme deux extrêmes.

	Degrés de liberté	Variance	Quotient
Variation entre Juin-Juillet et Août (classes superord.)	1		
Variation intraclasse	53		
Variation entre midi et soir-nuit	2	209.7	}10.2***-8.9***
Variation intraclasse	51	20.51—23.45	
Somme	54		

Il faut peut-être exclure les épreuves de juillet (dont le nombre est très bas) à cause des faits obtenus dans l'analyse du cycle annuel des *Diaptomus* et retenir comme classes superordonnées: Juin et Août. Dans ce cas, le quotient de variance devient 10.9 ***—9.4 ***.

Les épreuves qui entrent dans l'analyse de la migration diurne des *Cyclops* sont aussi prises dans le bassin central de Ottsjön. A cause des épreuves 15.6, 5 m. et 22.8 station D, 20 m. et l'épreuve près du fond, quelques valeurs ci-dessous sont données comme deux extrêmes.

L'analyse des épreuves près de la surface est donnée dans le tableau suivant.

Forme	Date	Partie du jour	Moyenne	Nombre des épreuves	Variance entre les classes	Variance intraclasse	Quotient	
Copépodites jeunes ...	15.6, 26.8, 28.8 1950	midi soir-nuit	1.8	10	}224.5	31.5 — 35.95	7.1*—6.2*	
	16.6, 30.8 1950		8.5	10				
Copépodites âgés	15.6 1950	}midi	2.4	9	}0.7	10.0	< 1	
	11.8, 20.8 1951		}soir-nuit	2.0				6
	16.6 1950 15.8 1951							
Adultes ...	15.6, 4.7, 22.8, 26.8, 28.8 1950	}midi	1.2	22	}51.97	11.25—11.40	4.6*	
	11.8, 20.8 1951		}soir-nuit	3.4				21
	16.6, 4.7, 5.7, 22.8, 30.8 1950							
	15.8 1951							

Il est probable qu'ordinairement le changement de l'abondance des adultes n'est pas aussi insignifiant que le montre le tableau parce que les épreuves de midi de 1951 sont prises par jours venteux quand la pauvreté du plancton dans la couche près de la surface est combattue par le vent. Cependant il faut que ces épreuves entrent dans l'analyse autrement le nombre des adultes devient trop petit.

Analyse plus complète pour les *Cyclopes* adultes. La classification est faite par profondeur et par date (le 22.8.1950 le soir et le 26.8.1950 le midi).

La somme des adultes pour les différentes classes ressort du tableau suivant. Il y a trois épreuves pour chaque classe.

	Surface	2 m.	5 m.	10 m.	15 m.	20 m.	Près du fond	Moyenne
22.8	5	33	20	40	39	11	2	7.2
26.8	0	63	22	8	9	9	4	5.5

	Degrés de liberté	Variance	Quotient
Variation entre les jours	1	36.59	1.2
Variation entre les profondeurs	6	165.9 — 164.4	5.4*** — 5.3***
Interdépendance	6	73.71 — 73.27	2.4
Variation intraclasse	28	30.69 — 31.12	
Somme	41		

» Quotient » donne les quotients entre la variance des trois premières lignes et la variance intraclasse.

La valeur inférieure de la variance de l'interdépendance prouve que la répartition aux différentes profondeurs est la même les deux jours, c'est à dire qu'on ne peut pas prouver l'existence d'une migration diurne avec ces épreuves.

Les épreuves de Hottön les: 25.8 et 26.8.1948 peuvent illustrer la migration diurne des Cladocères. Les épreuves de Ottsjön 1950 de pleine nuit, sont trop rares pour illustrer la migration diurne. On peut observer que les épreuves du soir 1950 ne montrent pas aussi clairement une accumulation vers la surface comme elles le font pour les *Diatomus*. Ci-dessous les moyennes pour les épreuves de surface et celles prises près du fond dans Ottsjön 1951. Le nombre des animaux près de la surface, le jour et près du fond, la nuit, est trop bas pour admettre une analyse de la variance mais néanmoins la migration diurne doit ressortir assez clairement de ces épreuves de 1951.

Date	Partie du jour profondeur	Daphnies	Bosmines	Nombre des épreuves
11.8, 20.8	midi surface	1.0	0	6
15.8	nuit »	2.0	12.7	3
11.8, 15.8, 20.8	midi près du fond	4.3	45.5	11
15.8	nuit » » »	0.7	1.3	3

La répartition les jours calmes. Le matériel ne suffit pas pour donner une image de la validité générale de la répartition des *Diatomus* aux différentes profondeurs les jours calmes. L'analyse de l'effet du vent a certainement indiqué que cette répartition diffère d'une répartition 1, 1, 1, 1, pour les épreuves près de la surface, (2 m.), 5 m. et 10 m., mais les données de cette analyse ne permettent pas une généralisation.

Pour les *Cyclops nauplii*, voici le tableau des sommes pour les profondeurs différentes: Il y a 3 épreuves chaque jour par profondeur.

Date	Surface	2 m.	5 m.	10 m.	15 m.	20 m.	Près du fond
14.8.50	24	—	89	76	77	180	134
26.8.50	1	38	58	82	84	127	178

Date	Variance entre les profondeurs	Variance intraclasse	Quotient
14.8.50	966.0	71.25	13.5***
26.8.50	1,128	105.7	10.7***

Il ressort de ceci que les nauplii préfèrent les couches profondes. Ce qui est aussi confirmé dans la plupart des autres séries de tous les lacs où ont eu lieu les recherches (Voir les tableaux). Cependant il est intéressant de noter la répartition «anormale» du 15.7.50, dans Ottsjön, la même série qui a causé des difficultés dans l'analyse de la répartition des Cyclopes copépodites âgés.

L'analyse de χ^2 (l'effet du vent), montre que les copépodites évitent la surface les jours calmes. Aucune autre généralisation ne peut être suffisamment bien fondée pour les copépodites.

L'analyse de la migration diurne des Cyclopes adultes, les 22.8. et 26.8.1950 (tableau p. 84) a déjà montré que les animaux évitent la surface et les couches les plus profondes les jours calmes et le soir. A cause de la migration diurne indistincte, les séries du soir sont caractérisées par la même répartition que celle du jour. L'analyse de l'effet du vent montre aussi que les adultes évitent la surface les jours calmes.

L'hypothèse concernant la répartition des Cladocères qui était proposée dans les renseignements préliminaires contenait: un rassemblement de Cladocères dans les couches du thermocline et un rassemblement près du fond dans les lacs qui manquent de thermocline. Le matériel donnait à penser que les Daphnies adultes femelles — une minorité — différaient de la règle discutée et étaient rassemblées dans les couches supérieures.

Dans les tableaux qui suivent, les Bosmines sont traitées comme une unité (il faut observer que les mâles sont très rares), mais les Daphnies femelles adultes sont séparées des autres Daphnies (voir chapitre: VII, Classification). Les Daphnies mâles sont aussi détachées comme un groupe à part, quand cela est possible, mais il faut savoir que les mâles très petits ne sont jamais séparés des autres Daphnies jeunes.

Parmi les séries d'épreuves prises après les renseignements préliminaires étaient apparues les séries de Ånn, 23.8.48, de Gesten 26.8.48, 4.8. et 16.8.1951, lacs ordinairement sans thermocline, qui ne peuvent pas être traitées statistiquement mais font observer que les dates vont bien avec l'hypothèse des renseignements préliminaires. Le rassemblement dans Gesten 1951 est

certainement au dessus de la couche la plus profonde mais il existait aussi ces jours là un indice de stratification thermique.

Analyse de la répartition dans Hottön le 23.8.50. Le thermocline correspond à 15—20 m. de profondeur:

	Daphnies mâles distinguaibles	Daphnies femelles jeunes et mâles indistinguaibles	Bosmines.
I Variance entre les profondeurs ...	188.5	64.25	168.8
II Variance entre 15—20 m. d'une part et autres profondeurs	678.4	133.4	260.7
III Variance intraclasse	73.17	58.12	67.42
Quotient entre II et III	9.3**	2.3	3.9
P entre:		0.2—0.1	0.1—0.05

Chaque profondeur est représentée par trois épreuves, sauf: 25 m. (deux) et 35 m. (une épreuve). Pour chacun des trois groupes discutés dans ce tableau les épreuves de 15—20 mètres contiennent environ la moitié de tous les individus obtenus dans ces séries. Les Daphnies femelles adultes sont trop rares pour établir un traitement statistique mais elles sont essentiellement obtenues dans les épreuves de 2, 5, 10 et 15 m.

Analyse pour Håckren les 5.8. et 17.8.1951 (le thermocline correspond à la région entre 5 m. et le fond 5.8. resp. 10 m. et le fond 17.8.):

	Daphnies femelles jeunes et mâles indistinguaibles le 5.8	Bosmines le 5.8	Daphnies femelles jeunes et mâles indistinguaible le 17.8
I Variance entre les profondeurs	557.5	11,988	1,017
II Variance entre thermocline et autres profondeurs	640.0	13,250	2,151
III Variance intraclasse	352.0	8,596.7	1,026
Quotient entre II et III	1.8	1.5	2.1
P entre	0.3—0.2	0.3—0.2	0.2—0.1

Presque toutes les Bosmines et Daphnies femelles jeunes, et les mâles indistinguaibles obtenus dans ces séries sont obtenus dans le thermocline (165 Daphnies sur un total de 195, le 5.8. — 162 sur un total de 185, le 17.8. — et 558 Bosmines sur un total de 564, le 5.8.). La variance intraclasse est donc si grande qu'elle rend les quotients petits et cela est aussi valide pour Hottön. Si on réuni les valeurs obtenues dans Håckren 5.8.51 et 17.8.51 et Hottön 23.8.50 et estime la différence entre thermocline et autres profondeurs pour ce groupe, le quotient pour les Daphnies mâles et femelles jeunes reçoit ** et celui pour Bosmina *. Peut-être que les quotients qui étaient calculés dans les renseignements préliminaires pour Hottön doivent être changés parce que le thermocline était mal défini. Le thermocline intéresse la couche de 15 à 20 mètres. Dans ce cas les quotients deviennent moins

significatifs (*). Les quotients pour *Bosmina* dans ce matériel (Hottön 25.8.1948) reçoivent un quotient avec ***, alors qu'ils n'étaient pas calculés auparavant.

Le rassemblement des valeurs inférieures de P, pour Hottön et Håckren peut servir en tant que preuve définitive pour l'hypothèse.

Le 5.8. et le 17.8.1951, 102 Daphnies femelles adultes sont obtenues dans Håckren, 2 m., sur une totalité de 144 Daphnies femelles adultes ces jours là. Cependant le quotient entre la variance entre les profondeurs et la variance intraclasse est seulement de 1.8., $P=0.2$ (le 17.8.).

Les Daphnies mâles et les femelles jeunes de Ottsjön sont groupées comme suit: (les groupes empiètent les uns sur les autres).

I. Les Daphnies femelles jeunes et les mâles indistinguables (qui sont trop petits pour être reconnus comme mâles) les 17.8., 25.8., 26.8., 28.8.1950 et 11.8., 20.8.1951. Epreuves de jour, prises dans le bassin central (station A, B, C, D) Profondeur: surface, 2, 5, 10, 15, 20 m. et près du fond. Nombre total des épreuves: 101. Sur un total de 81 individus 46 sont obtenus dans les épreuves prises près du fond.

II. Les femelles jeunes et les mâles (jeunes et adultes) les 4.7., 15.7., 23.7., 14.8., 17.8., 25.8., 26.8., 28.8.1950 et les 11.8., 20.8.1951. Epreuves prises dans les mêmes stations que pour I. Nombre total des épreuves: 135. Profondeur: surface, 5, 10, 15, 20, près du fond. 102 individus sur une totalité de 198 sont pris près du fond. Pour les séries prises en juillet, une telle accumulation n'est pas caractéristique. En août, 35 mâles, sur une totalité de 43 sont obtenus près du fond — c'est à dire les mâles qui peuvent être reconnus comme tels.

III. Les mêmes formes que pour II, mais seulement les dates données pour I (17.8.1950 et plus tard). Les profondeurs comme pour I. Nombre total des épreuves, aussi 101. Sur une totalité de 124, 81 individus sont obtenus près du fond.

	I	II	III
a Variance entre les profondeurs	Pas calculé nombre trop bas	46.74	47.35
b Variance entre épreuves près du fond et autres profondeurs	81.70	226.1	279.6
c Variance intraclasse	4.14	5.71	3.12
Quotient entre b et c	19.7***	39.7***	89.7***

Les Bosmines dans Ottsjön sont groupées selon les dates.

I. Les épreuves prises les 10.6., 15.6., 15.7. et 14.8.1950 aux stations A. — Nombre total des épreuves: 65. — Profondeurs: surface, 5, 10, 15, 20 m. et près du fond. — 288 individus sur une totalité de 471, sont pris près du fond. A cause du nombre irrégulier des épreuves dans les classes, le problème est analysé comme si c'était une division hiérarchique.

II. Les épreuves prises les 17.8., 25.8., 26.8., 28.8.1950 et les 11.8., 20.8.1951.

— Stations A. B. C. D. (bassin central). — Nombre total des épreuves: 101.
 — Profondeurs: comme pour A, plus une à 2 m. — 304 Bosmines sur une
 totalité de 321 étaient prises près du fond.

I	Degrés de liberté	Variance
Variation entre les jours	3	14.9
Variation intraclasse	61	117-118
Variation entre les profondeurs	20	329.7
Variation intraclasse	41	15.95-17.17
Somme	64	
Quotient $\frac{329.7}{15.95} = 20.7^{***}$ $\frac{329.7}{17.17} = 19.2^{***}$		

II	Degrés de liberté	Variance
Variation entre les profondeurs	6	793.9
Variation entre les épreuves prises près du fond et autres profondeurs	1	4,759
Variation intraclasse	94	183.4
Somme	100	
Quotient $\frac{4,759}{183.4} = 26^{***}$		

Les épreuves prises les 17.8., 25.8., 26.8., 28.8.1950 et les 11.8., 20.8.1951
 dans le bassin central (stations A, B, C, D) sont traitées en regard des
 Daphnies femelles adultes. — Nombre total des épreuves 101.

Somme des individus pour les différentes profondeurs:

	Surface	2 m.	5 m.	10 m.	15 m.	20 m.	Près du fond
S (x)	15	44	27	15	11	10	I
Nombre des épreuves	16	14	14	14	14	13	16

	Degrés de liberté	Variance
Variation entre les profondeurs	6	14.68
Variation entre 2 m. et autres profondeurs	1	61.22
Variation intraclasse	94	3.459
Quotient $\frac{61.22}{3.459} = 17.7^{***}$		

Evidemment le rassemblement de Daphnies femelles adultes à 2 m. dans
 Håckren était réel et non pas l'effet du hasard de même que la pauvreté vers
 le fond.

Un minimum de Cladocères, toutes formes, près de la surface est déjà
 montré dans l'analyse de l'effet du vent pour les épreuves entre la surface
 et 10 m.

Le cycle annuel

Il est très improbable que la variance entre séries prises à des jours différents ne soit pas plus grande que la variance dûe au hasard, du moins si les jours sont séparés par exemple, par une semaine. Même si le recrutement et la mortalité sont à peu près de même grandeur, les deux facteurs ne doivent que très rarement se contrebalancer. Cependant la variance intraclasse qui ressort de l'analyse suivante contient bien sur plus que la variance dûe au hasard. Grâce au nombre insignifiant de planctons dans plusieurs épreuves, il est souvent nécessaire de juxtaposer les épreuves d'une série dans une seule classe pour obtenir une somme (x) plus grande que 15 (voir page 80). Dans ce cas la variance entre profondeurs différentes est incluse dans la variance intraclasse. Si on peut malgré cela montrer des différences significatives entre jours différents, on peut pourtant douter de ce que ces différences correspondent à un changement de l'abondance de la totalité de la population parce que les échantillons peuvent être pris là où il ne convient pas, c'est à dire qu'aucun échantillon n'est pris à la profondeur où sont rassemblés les planctons.

Pour les *Diaptomus* adultes suit les quotients entre variance entre des séries et variance intraclasse. Les séries sont prises au station A dans Ottsjön 1950 (milieu du jour).

Date des séries ...	10.6	15.6	4.7 + 15.7	23.7	14.8	17.8 + 25.8
Vent	Fort	Faible	Faib. Fort	Calme	Faible	Fort Fort
Moyenne	4.9	3.1	0.58	3.3	1.4	0.67
Quotient	2.1—4.0	14***—34***	25***	2.9—2.6	1.6—1.4	
P entre	0.2—0.05			0.2—0.05	(environ 0.2)	

A cause des épreuves 15.6. (surface) et 14.8. (20 m.) quelques quotients sont donnés comme deux extrêmes.

En raison du fait discuté ci-dessus il faut juger avec précaution les résultats obtenus ici avec l'analyse de variance. Pourtant dans tous les cas la probabilité que les différences sont dues au hasard est petite; si la différence n'a pas toujours une signification méritant le signe ***, la probabilité que les différences peuvent être provoquées par hasard n'est pourtant jamais plus grande que $P=0.2$. On a évidemment un rassemblement de valeurs de P inférieures; considérant le fait que la variance intraclasse contient la variance entre des profondeurs différentes, on ne peut pas nier que la plupart des différences entre moyennes de jours différents sont réelles. Mais est-ce que ces différences sont dues à une distribution inopportune des échantillons comme on l'a proposé plus haut? S'il y a un rassemblement

des animaux dans les couches supérieures, il doit être dispersé les jours venteux et s'il y a un rassemblement dans les couches profondes le jour, il doit être dispersé le soir et la nuit. Retournons au matériel actuel.

Le maximum en juin doit être valide (pris en partie par jours venteux).

L'existence d'un minimum en juillet est très probable (les épreuves sont prises en partie par vent fort et aucun rassemblement de *Diaptomus* le soir et la nuit des 4.7. et 5.7., dans les couches superficielles, n'est obtenu).

Il est difficile de juger quelle série entre le 23.7.50 et le 30.8.50 représente le mieux l'abondance du *Diaptomus* dans le bassin central de Ottsjön.

Dans l'analyse du cycle annuel des *Cyclops* pour Ottsjön, le traitement statistique dans toutes les phases n'est pas recherché. Quand les animaux manquent complètement pendant une époque, l'analyse de la variance est impossible à faire mais elle est aussi moins nécessaire.

Forme	Dénomination	Date	Vent	Moyenne	Station
Nauplii	I a	12.5.50	Fort	6.2	A
	b	26.5.50	»	1.5	»
	II a	26 + 27.5.50	Fort et calme	2.2	»
	b	10 + 15.6.50	Fort et faible	0.59	»
Copépodites jeunes ...	III a	12.5.50	Fort	9.0	»
	b	10.6.50	«	26	»
Copépodites âgées	IV a	26 + 27.5.50	Fort et calme	2.6	»
	b	10 + 15.6.50	Fort et faible	0.83	»
	V a	15.6.50	Faible	1.3	»
	b	4.7.50	»	13	A, 13h
Adultes	VI a	11.8.51	Fort	5.7	A, C, D
	b	20.8.51	»	3.0	» » »
	VII a	27.5.50	Calme	3.7	A
	b	4.7.50	Faible	2.0	A, 13h
	c	14.8.50	»	7.6	A
	VIII a	10.6.50	Fort	6.3	»
	b	15.7.50	»	1.8	»
	c	17.8.50	»	8.7	A, 13h
IX a	a	11.8.51	»	4.5	A, C, D
	b	20.8.51	»	7.2	» » »

Dans le tableau ci-dessus les différences entre séries ont été traitées deux par deux.

Comparasion:	I a-b	II a-b	III a-b	IV a-b	V a-b	VI a-b
Variance entre les classes	151.6	29.73	1.980	35.32	556.9	80.18
Variance intraclasse	5.90	2.98	30.46	3.17	15.86	11.15
Quotient	26***	10**	65***	11**	35***	7.4**

Comparaison:	VII a-b	VII b-c	VIII a-b	VIII b-c	IX a-b
Variance entre les classes	9.49	138.9	140.5	336.2	79.6
Variance intraclasse	3.04	9.02	2.88	1.27	9.97
Quotient	3.1	15***	49***	265***	8.0**
P	0.2 —0.05				

Différentes stations d'un même lac

Si on est forcé de juxtaposer dans une même classe toutes les épreuves d'une station et d'une journée pour obtenir une somme des variables assez forte pour faire une comparaison avec d'autres stations (analyse de la variance) on trouve souvent que la variance intraclasse devient si grande que la différence entre les classes n'est pas significative. Le quotient de variance entre les classes et intraclasse est même souvent plus petit que I. On peut donner comme exemples soit: une comparaison entre stations A et C+D, dans Ottsjön, le 11.8. ou 20.8.1951, pour les Cyclopes nauplii, copépodites âgés et adultes, ou une comparaison entre les stations A et D, dans Hottön, le 10.5.1948, pour les Cyclopes nauplii. La possibilité de montrer les différences entre les stations augmente si on peut tellement bien grouper le matériel que les épreuves prises à chaque profondeur forment une classe.

L'analyse des *Diaptomus* adultes est faite selon la méthode moins opportune dont il vient d'être parlé. Le matériel est traité comme si il existait une division hiérarchique. I, II, III, sont les trois groupes superordonnés.

I			II			III		
Station	Date	Moyenne	Station	Date	Moyenne	Station	Date	Moyenne
A	14.8.50	1.4	A	17.8.50	0.67	A	26.8.50	2.4
M, N, O ...	15.8.50	0.83	E	17.8.50	2.8	B, C, D ...	26.8.50	0.76

	Variance	Degrés de liberté
Variation entre I, II et III		2
Variation intraclasse		76
Variation entre A et B, C, D, E, M, N, O	12.87	3
Variation intraclasse	4.18 = 4.37	73
Somme		78
$\frac{12.87}{4.18} = 3.1^*$	$\frac{12.87}{4.37} = 3.0^*$	

A cause des épreuves de 20 m. du 14.8., les deux extrêmes sont données ci-dessus. Les *Diaptomus* adultes sont plus nombreux dans les épreuves prises près de la surface au dessus de la grande profondeur que dans les épreuves prises près des rives (se rapporter au tableau 9, Ottsjön, juillet et août 1950) mais il n'est pas donné une expression statistique de ce phénomène.

On peut pour les *Cyclops* nauplii, copépodites jeunes ou adultes, grouper les nombres obtenus dans Ånn le 8.5.1948, selon deux principes:

1. — Nombre, dans les épreuves prises près du bord de la glace et dans les épreuves prises en eau libre.
2. — Nombre, dans les épreuves prises aux différentes profondeurs.

C'est évidemment un problème à division collatérale.

	Nauplii	Copépodites jeunes	Copépodites âgés
Variance entre épreuves prises près de la glace et en eau libre	0.04	1.64	7.50
Variance entre profondeurs	0.94	15.4	6.94
Interdépendance	3.72	20.2	14.8
Variance intraclasse	5.73	8.60	12.1

Aucune différence n'est significative.

Le même traitement est poursuivi pour les *Cyclopes* nauplii et adultes dans Ottsjön 1950. Les épreuves sont prises le jour, sauf le 22.8. (soir) mais la migration diurne des *Cyclopes* est reconnu comme insignifiant.

Nauplii	{ Station A 22.8, 25.8, 26.8 Moyenne 29.5	Station C 26.8, B 26.8, D 28.8 Moyenne 25.4
Adultes	{ Station A 22.8, 25.8, 26.8 Moyenne 6.6	Station D 22.8, 26.8, 28.8 Moyenne 5.0

	Nauplii	Adultes
Variance entre station A et autres stations	172.0	27.52
Variance entre les profondeurs	1,194	78.33—79.77
Variance de l'interdépendance	47.97	25.25—21.80
Variance intraclasse	172.4	28.88—29.31

La différence entre la station A et les autres stations n'est pas significative. Les différences entre les profondeurs:

$$\frac{1,194}{172.4} = 6.9^{***} \quad \frac{78.33}{28.88} = 2.7^* \quad \frac{79.77}{29.31} = 2.7^*$$

En ce qui concerne «la fuite des rives» le nombre des *Cyclopes* nauplii, copépodites ou adultes est plus petit dans les épreuves prises près des rives que dans les épreuves prises près de la surface au dessus de la grande profondeur dans Gesten 4.8., 5.8.1951, Ottsjön 4.7., 5.7. et 17.8.1950 mais il y a aussi des exemples contraires et des cas où les deux régions sont vides de *Cyclopes*. Le matériel est insuffisant pour une analyse mais on peut remarquer comment une seule épreuve (station P le 28.7.50, Ottsjön) peut être extrêmement riche près des rives et combattre la pauvreté dans les autres épreuves.

Les nombres des *Daphnia* dans Ottsjön (août 1950) sont analysés comme suit:

Station A 22.8, 25.8, 26.8	Moyenne 4.8
Station C 22.8, 26.8, B 26.8, D 22.8, 26.8, 28.8	Moyenne 2.8

Les épreuves sont prises le jour, sauf le 22.8. (soir). L'analyse est faite comme s'il existait une division hiérarchique.

	Degrés de liberté	Variance
Variation entre les profondeurs	6	
Variation intraclasse	56	
Variation entre station A et autres stations	7	38.10
Variation intraclasse	49	10.63
Somme	62	

$$\frac{38.10}{10.63} = 3.6^{**}$$

Les *Bosmina* atteignent de temps en temps une grande richesse dans les épreuves prises près des rives (voir Ottsjön 21.8. station Y) on peut parler de véritables essaims.

Une «fuite des rives» qui donnerait une pauvreté de Cladocères plus grande que celle de la surface de la région pélagique, peut à peine être montrée avec le matériel.

En général les épreuves prises aux stations autres que celles du bassin central des lacs actuels servent seulement à donner un aperçu des différences entre les stations du même lac.

A la fin de ce souschapitre, il faut remarquer combien la situation est complexe. TONOLLI (1949 c) a constaté que les individus des collections de planctons dans les différentes stations sont dans un perpétuel échange mutuel. S'il existe des différences significatives entre les moyennes des différentes stations, ces différences peuvent être dépendantes des qualités caractéristiques des différentes stations, mais cela n'est pas nécessaire. Si le plancton forme des essaims (répartition *bunched* comme le dit RICKER, 1938) qui ne sont pas dépendants des qualités différentes des stations différentes, la conséquence en est peut-être qu'il y a des différences significatives entre les moyennes d'une même station aux différents jours, même quand la population n'est pas influencée par les facteurs qui règlent le cycle annuel ou la migration diurne.

V. Copépodes: Diaptomus

Les nauplii et les copépodites les plus jeunes, classifiés comme Diaptomus, peuvent être Hétérocopes aussi, mais en regard des différents cycles annuels de Diaptomus et d'Hétérocopes et la présence insignifiante d'Hétérocopes, on peut ignorer cette source d'erreur.

Le cycle annuel

RUTTNER (1930) a montré que chacune des différentes formes de l'ontogénèse, du *Diaptomus gracilis*, SARS, existent la plus grande partie de l'année dans le Lunzer Untersee. La période de propagation est longue. Pourtant il y a un cycle annuel car chacune des différentes formes (nauplii, copépodites, et adultes) disparaissent une fois par an et réapparaissent dans les mois suivants; les copépodites après les nauplii et les adultes après les copépodites. Les intervalles entre les réapparitions indiqueraient peut-être la vitesse de l'ontogénèse. Il est évidemment difficile d'analyser la longueur de la vie des individus.

L'existence d'oeufs durables chez les *Diaptomus* (WOLF, 1904: *D. castor* et *D. coerulus*. HAECCKER, 1902: *D. denticornis*. EKMAN, 1904: *D. laciniatus*, *denticornis*, *laticeps* et *graciloides*. TONOLLI, 1949 a: *D. bacillifer*) montre qu'il existe des saisons dont le milieu est défavorable dans les lacs où les oeufs sont produits. Plusieurs auteurs ont étudié le plancton dans des milieux extrêmement froid; on peut espérer y observer un cycle annuel de *Diaptomus* plus simple à analyser que celui de Lunzer Untersee puisque le milieu doit être défavorable la plus grande partie de l'année. On peut supposer que dans cette partie de l'année le *Diaptomus* existe comme oeuf durable et que le nombre de générations est réduit au minimum, la saison favorable étant si courte. Tous les individus doivent passer les différentes phases de l'ontogénèse en même temps, la phase de l'ontogénèse étant la même pour tous les individus pendant la longue saison défavorable, à savoir: Oeufs durables.

EKMAN (1904) constate que la propagation des *Diaptomus laticeps*, SARS, dans les grands lacs des hautes montagnes de Suède, arrive deux mois après la débacle. Il donne l'existence d'une seule génération par an pour le *D. laciniatus*, LILLJEBORG, le *D. denticornis*, WIERZEJSKI, et pour le *D. graciloides*, LILLJEBORG, dans les petits lacs, mais deux générations dans les grands lacs pour *D. graciloides*. Il constate en outre que l'ontogénèse prend deux mois environ pour les trois dernières espèces à partir de leur éclosion jusqu'à l'apparition des oeufs dans les sacs ovigères des femelles. EKMAN cite des auteurs qui ont étudié l'ontogénèse des trois mêmes espèces en Europe Centrale et constate que l'ontogénèse est plus rapide en Suède. Les faits relevés par RUTTNER (1930) confirment que l'ontogénèse est moins rapide en Europe Centrale. Cela ce sont les faits actuels pour le travail présent, obtenus par des auteurs qui ont étudié l'abondance du plancton dans les lacs. Il faut seulement ajouter que TONOLLI (1949 a) a amélioré la méthode en étudiant plusieurs caractères de la morphologie des adultes. Il a pu distinguer les néoadultes et les vieux spécimens et il a pu analyser la population plus profondément.

D'autres auteurs ont attaqué le problème selon une autre méthode. Ils ont cultivé les *Diaptomus* en laboratoire. WALTER (1922) constate que le *Diaptomus vulgaris*, SCHMEIL, éclot en février arrive à maturation sexuelle après un mois environ et vit dix mois. Pour les individus éclots en Mai, les chiffres correspondants sont: un mois et demi et treize mois. DIETRICH (1915) constate que le minimum entre le temps de l'éclosion et de la maturation sexuelle est de 29 jours en laboratoire pour le *Diaptomus vulgaris* et *Wierzejskii*, RICHARD.

Sans doute y a-t-il d'autres auteurs qui ont discuté de l'onthogénèse du *Diaptomus*, mais l'auteur par le choix qu'il a fait veut montrer:

1. — combien le cycle annuel est de temps en temps difficile à analyser au moyen des recherches sur l'abondance des *Diaptomus* dans les lacs.
2. — qu'il existe des recherches sur la longueur de l'onthogénèse qui doivent être valides dans le milieu naturel ou expérimental étudié par les auteurs.
3. — Qu'on a observé des valeurs très différentes sur la longueur de l'onthogénèse du *Diaptomus*.

Quelles sont les conditions essentielles qui dirigent la vitesse de l'onthogénèse?

Selon EKMAN, op.cit., il y a des différences profondément fondées (sans doute héréditaires) entre les populations du Nord de la Suède et celles de l'Europe Centrale. Mais pour comprendre les différences entre les lacs du Jämtland il est plus actuel de discuter les modifications qui peuvent être provoquées par des milieux différents. Plusieurs auteurs (DIETRICH 1915, RUTTNER 1930) subordonnent l'accélération de la vitesse de l'ontogénèse à une augmentation de la température. Cela est sans doute valide en tant que généralisation large et dans ce chapitre est employé comme tel. Quant aux résultats des études de COKER (1933) sur les Cyclopes, on doit accepter l'influence de l'abondance en nourriture sur l'ontogénèse des *Diaptomus*, comme une hypothèse très probable. DIETRICH (1915) a proposé aussi l'espace comme influence importante sur l'ontogénèse.

Il faut à présent discuter une objection qui pourrait être faite aux conclusions de ce chapitre.

Si l'on observe une alternance entre maxima et minima dans l'abondance des *Diaptomus* adultes, il n'est pas nécessaire que cela soit regardé comme la conséquence d'une alternance de l'éclosion de nauplii, cela peut aussi être l'expression d'une alternance entre milieu défavorable et favorable pour les *Diaptomus* adultes (action des animaux de proie, abondance en nourriture, etc.) En d'autres mots, le rythme de l'abondance des *Diaptomus* peut être l'effet soit du recrutement soit de la mortalité (voir RUTTNER 1930, page. 66).

Dans les cas actuels, les maxima en nauplii sont remplacés par des maxima en copépodites et ceux-ci, plus tard, par des maxima adultes. Cela doit donc être un véritable effet d'ontogénèse simultanée pour la plus grande partie de la population.

Ottsjön. Propriétés générales du cycle annuel. — On peut voir (Graph. 16) que la composition des épreuves pour les différentes années coïncide substantiellement au même cycle annuel. Donc le rythme annuel du graphique est un rythme réel. Ce qui est aussi confirmé dans le chapitre IV.

Dans les épreuves d'hiver, le *Diaptomus* est seulement représenté par des nauplii (16.2.1947, 30.3.1946). L'épreuve du 30.3.1946 n'a pas été prise avec un chercheur mais avec un filet à mailles d'environ 150—200 μ . Seuls des nauplii isolés furent pris, mais la grandeur des mailles du filet pouvait permettre aux nauplii de s'échapper. Au temps de la débacle (9.5.1948, 12.5.1950), le nombre de nauplii est réduit et le nombre de copépodites, augmenté. On voudrait pouvoir discuter ce fait, que le nombre de copépodites semble excéder le nombre de nauplii en hiver, mais on y est empêché pour la raison suivante: les épreuves d'hiver et de débacle sont prises à des années différentes. Cependant après la débacle de 1950, le nombre de nauplii se multiplie, sans qu'aucun *Diaptomus* adulte ne s'y soit encore vu. Les nauplii doivent donc éclore des oeufs durables.

A présent on peut introduire dans la discussion la relation entre nauplii en hiver et copépodites au temps de la débacle: les copépodites se sont probablement accumulés avant la débacle parce que des oeufs durables ont successivement éclot et les nauplii évolués en copépodites dans le cours de l'hiver.

Les copépodites des *Diaptomus* ne sont pas classifiés dans les copépodites jeunes et âgés comme les copépodites des Cyclopes, mais les copépodites du 12.5.1950, sont évidemment plus jeunes que ceux du 26.—27.5. et du 10.—20.6.1950. Le 5.6.1946 et le 10.6.1950, apparaissent les premiers adultes. Vraisemblablement le maximum dans la courbe copépodites ne représente pas le nombre total de copépodites qui existaient cette année là, parce que les premiers copépodites se sont transformés en adultes avant que le supplément de copépodites de nauplii soit encore terminé. Après le milieu de Juillet, les nauplii et les copépodites ont disparu des épreuves pendant tout le reste de l'été.

Des femelles adultes, portant des oeufs ne sont observées qu'après le 17.8. Les *Diaptomus* éclot pendant l'hiver et le printemps vivent ainsi au moins quatre mois et probablement plus et l'intervalle entre l'éclosion et l'apparition des oeufs dans les sacs ovigères des femelles est de plus de deux mois, peut être entre trois et six mois.

Le matériel ne suffit pas pour rendre compte de la population *Diaptomus* pendant l'automne.

Discutons la question du minimum d'adultes en Juillet.

L'aspect statistique est traité au chapitre IV. La diminution à la fin de Juin peut être provoquée par une migration vers les rives ou par une forte mortalité; l'augmentation du nombre d'adultes pendant Juillet peut être l'effet d'une migration vers le centre du lac où grâce à la plus haute température, les nauplii et les copépodites passent très vite les différentes phases de croissance, si vite, que leur nombre est toujours très rare dans une situation momentanée et deviennent adultes. Aucune des hypothèses ne peut être éclaircie avec le matériel présent.

Ottsjön: Variations entre années différentes. — Les années 1948 et 1950 avaient environ la même date de débacle et les épreuves du 9.5. 1948 et du 12.5.1950 étaient prises très tôt après la débacle; leur composition se ressemblaient pourtant beaucoup avec cette différence que les copépodites, en 1948 étaient substantiellement jeunes, mais en 1950, ils étaient en partie jeunes et en partie âgés. En 1946, la débacle arriva fin Mai, donc beaucoup plus tardivement et fut suivie d'une semaine extraordinairement chaude. Cette semaine étant exceptionnellement peu venteuse, l'eau dans Ottsjön jusqu'à 10 mètres de profondeur était plus chaude que l'eau profonde. Sauf trois nauplii, tous les animaux étaient rassemblés dans l'eau chaude. L'existence d'un individu adulte peut indiquer que la phase de l'évolution de la population était plus avancée que les 26.—27.5.1950, c'est à dire que l'ontogénèse a été plus rapide en 1946, si on prend la débacle comme point identique durant les différentes années. Cette interprétation s'accorde avec la conception de l'interdépendance entre la température et la vitesse de l'ontogénèse discutée plus haut. En Août, les populations aux différentes années sont arrivées à peu près à la même phase.

Les autres lacs. — Les autres lacs font voir un rythme annuel de *Diaptomus* évidemment différent de celui de Ottsjön. Les épreuves ne sont pas du tout aussi nombreuses qu'en Ottsjön et l'analyse ne peut être poursuivie aussi efficacement (voir p. 79).

L'hiver (31.3.46) il y a des copépodites et aussi un exemplaire adulte dans les épreuves d'Ånn. C'est seulement en conformité avec cette situation que les épreuves autour de la débacle contiennent — sauf des nauplii et copépodites — quelques adultes dont des femelles portant des sacs ovigères. La même composition de plancton dans Ånn au printemps est relevée par les épreuves prises avec un filet. Les nauplii et copépodites en août sont probablement les descendants des adultes de mai — une fraction de la population *Diaptomus* qui n'existe pas dans Ottsjön. Les copépodites pendant l'automne

doivent appartenir à la même fraction. Les nauplii au printemps et les adultes en août correspondent évidemment à la fraction qui existe dans Ottsjön. Il est curieux qu'il puisse exister une fraction dans Ånn qui n'existe pas dans Ottsjön quoique les rythmes annuels de la température soient assez semblables. Evidemment le milieu hivernal dans Ånn permet aux copépodites et aux adultes de survivre. Un tel cas avec deux fractions d'une population sera plus profondément discuté dans le chapitre des Cyclopes.

Dans Hottön il existe un cycle annuel de Diaptomus encore plus complexe que celui dans Ånn. Les épreuves 9.3.50 contiennent seulement un nauplius. Une floraison de nauplii commence au printemps et aussi un adulte femelle portant des oeufs est observé (10.5.48). A la même saison commence les transformations des nauplii en copépodites. (Le 8.5.50 les copépodites ne sont pas encore apparus — le lac était encore couvert de glace et la température était de 1—2 degrés plus bas que le 10.5.48.) Il existe donc dans Hottön les deux fractions observées dans Ånn. Mais il n'y a pas de nauplii en août comme dans Ånn — probablement parce que cette fraction est faible dans Hottön — et le nombre de copépodites semble augmenter de juin jusqu'en août.

Cependant il faut remarquer que les copépodites dans Hottön en Juillet et en Août sont substantiellement pris dans l'eau froide de l'hypolimnion, sauf le 26.8.1948, dans une épreuve prise la nuit. Les migrations diurnes sont traitées plus bas; on peut d'abord remarquer que les migrations de Diaptomus sont souvent très accentuées. Cependant les migrations diurnes de tous les individus d'une population de planctons ne sont jamais réalisées sur une grande distance. On peut supposer qu'une fraction des copépodites existants au printemps s'est transformée en adultes déjà en Juin ou en Juillet parce que les individus demeurent dans l'eau chaude de l'épilimnion alors qu'une autre fraction se partage en migrations diurnes plus extrêmes, ce qui retarde leur ontogénèse. Cela peut contenir toute la vérité, parce que les copépodites dans Ottsjön se sont transformés en adultes en Juin dans l'eau d'une température d'environ 7 à 8 degrés et que cette température n'est pas obtenue avant Août dans l'hypolimnion de Hottön.

Les adultes dans Hottön ne sont jamais nombreux dans les épreuves, il est donc difficile de parler de maxima. Des adultes femelles portant des oeufs sont observés seulement en Octobre, sauf l'exemplaire de Mai. Nous avons évidemment une situation assez compliquée dans Hottön et les limites entre les fractions provoquées par le milieu hivernal semble pouvoir être nivellées pendant l'été.

La répartition aux différentes profondeurs. La migration diurne

En prenant les épreuves dans Ottsjön, le 10.6., 15.6., 16.6. et le 20.6.1950, l'auteur pouvait observer l'influence du vent sur la répartition des Diaptomus et l'interdépendance qui existait entre la répartition et les migrations diurnes.

Le nombre d'épreuves prises en surface et à 5 mètres le midi du 15.6.1950 étant trop peu nombreux, une série d'épreuves était prise le soir du 16.6. dans le but de compléter les premières épreuves. L'étude des épreuves a montré que les épreuves de surface du 16.6. contenaient beaucoup plus de *Diaptomus* adultes que celles du 15.6. Deux explications se présentent, à savoir: que la différence dépend ou des heures où les épreuves ont été prises, ou de la force différente du vent; le 15.6. le vent était faible et le 16.6., calme. On peut à peine objecter l'introduction de l'idée de migrations diurnes dans la discussion. Les migrations des *Diaptomus* sont très marquées selon plusieurs auteurs. (RUTTNER 1930, SOUTHERN GARDINER 1932, FINDENEGG 1943, PENNAK, 1944. HUITFELDT KAAS 1906, a même donné la sensibilité à la lumière comme facteur opérant une différence de répartition entre les jours ensoleillés et les jours de mauvais temps.)

Déjà les épreuves du 20.6. à midi, par une journée très calme, confirmaient que la différence entre le 15.6. et le 16.6. pouvait être comprise comme l'effet d'une migration diurne.

Il restait donc comme hypothèse à priori que le vent pouvait exercer un effet de nivellement sur l'inégalité de la répartition, inégalité produite par les migrations actives des planctons. On a supposé que l'effet du vent, c'est à dire l'effet de produire des courants, diminue vers le fond du lac. En conséquence la région entre la surface et dix mètres de profondeur est choisie pour examiner l'effet du vent.

L'effet nivellant du vent et l'existence d'une migration diurne sont prouvés dans le traitement statistique. Ici, il faut noter que l'accumulation en surface n'atteint pas le maximum à minuit, mais le soir (Ottsjön 21.8., 26.8.1950). RUTTNER (1930) a confirmé l'existence d'une migration du soir, migration engageant surtout les organismes dans les couches supérieures.

VI. Copépodes: Cyclopes

Le cycle annuel

Nous en savons beaucoup plus sur l'ontogénèse des *Cyclopes* que sur l'ontogénèse des *Diaptomus* grâce aux auteurs qui ont étudié les *Cyclopes* en laboratoire.

DIETRICH (1915) constate qu'une durée de 26 jours, comptés à partir de l'éclosion jusqu'à l'apparition des oeufs dans les sacs ovigères des femelles, est un minimum pour l'ontogénèse (*Cyclops strenuus* FISCHER, et *C. viridis* JURINE). Il remarque qu'en général une augmentation de température provoque une ontogénèse plus rapide, mais il souligne la grande influence de l'espace et cite aussi l'influence de la nourriture et d'autres facteurs.

WALTHER (1922) relève pour le *Cyclops viridis* un intervalle allant de 5 semaines à 5 mois pour l'ontogénèse jusqu'à la première apparition des

oeufs. La courte période se rapporte aux températures de 20 degrés à 30 degrés, la longue période se rapporte aux températures de quelques degrés au dessus de zéro. Après la première apparition des oeufs les femelles vivent environ 4 à 5 mois. La longueur de la vie des mâles est plus courte. Pour le *Cyclops serrulatus* FISCHER, elle montre que l'ontogénèse, jusqu'à la maturation sexuelle prend 2 semaines quand la température est la plus favorable (10 degrés), mais un mois et demi durant la saison froide.

Le travail de COKER (1933) traite de l'influence de l'abondance en nourriture sur l'ontogénèse quand la température est constante. Il constate qu'avec une bonne provision de nourriture le *Cyclops vernalis* FISCHER met entre 9 et 11 jours, par une température de 18 degrés, pour arriver à maturation sexuelle; le *Cyclops serrulatus* met entre 14 et 16 jours par 14 degrés; le *Cyclops viridis* femelle met entre 18 et 22 jours ou entre 38 et 52 jours (deux fractions) par 20—22 degrés. Il remarque que les Cyclopes peuvent arriver très vite au quatrième stade de copépodite, même quand la nourriture est extrêmement rare, mais dans cette circonstance, l'ontogénèse s'arrête-là et les animaux demeurent longtemps au quatrième ou cinquième stade de copépodite.

On peut dire en généralisant que l'ontogénèse devient plus rapide quand la température est élevée tant que la nourriture ne devient pas insuffisante. Ordinairement dans l'intervalle de température étudié ici pour les lacs du Jämtland, quand la température est la plus basse, la quantité de nourriture doit être la moins abondante. On peut supposer une corrélation positive entre la température et la vitesse de l'ontogénèse. Si la vitesse de l'ontogénèse est différente pour le même espèce de *Cyclops* dans des lacs très proches quant à la température, les résultats de COKER fournissent une hypothèse très bien fondée pour éclaircir ces différences.

Voyons à présent quelques résultats qui ont été obtenus dans les recherches faites au sujet de la faculté qu'ont les Cyclopes à survivre dans un milieu défavorable. Aucun auteur n'a prouvé l'existence d'oeufs durables chez les Cyclopes. CLAUS (1895) ayant prélevé, d'un lac à sec, de la terre qu'il humecta, put y étudier l'apparition des Cyclopes. Il constata leur apparition dans différentes phases de l'ontogénèse. WOLF (1904) le confirme et ROY (1932) a montré que les Cyclopes peuvent survivre quand le lac est desséché, au 4ème stade de copépodites ou comme adultes, en s'entourant d'une capsule.

D'après EKMAN (1904), les *Cyclops scutifer*, dans les petits lacs de la région des hautes montagnes de Suède, sont représentés par des nauplii, au temps de la débacle, qui deviennent adultes en 4 semaines, les femelles portant des oeufs. Ces générations sont suivies d'une autre la même année. La situation est plus complexe pour les grands lacs. Selon le même auteur, la population contient des nauplii, des copépodites et même quelques rares individus adultes au temps de la débacle.

Ottsjön. Propriétés générales du cycle annuel. — Dans les deux séries d'épreuves d'hiver, prises dans Ottsjön (30.3.1946, 16.2.1947), il y a des copépodites âgés et dans les épreuves de 1947, il y a aussi des nauplii. S'il existait des nauplii le 30.3.1946, cela est inconnu parce que le filet étant à mailles de 150 à 200 μ , les nauplii devaient pouvoir passer au travers.

Dans tous les lacs étudiés, les épreuves d'hiver contiennent des nauplii, des copépodites âgés et seulement de rares copépodites jeunes, jamais d'adultes. On peut constater que le *Cyclops scutifer* passe l'hiver comme nauplius et comme copépodite, surtout comme copépodite âgé. On peut préciser en disant que l'évolution des oeufs et des nauplii est tardive en hiver, et qu'il est possible que les oeufs produits par de très rares adultes, s'ajoutent de temps en temps au nombre de nauplii, de même qu'il est possible aussi que quelques nauplii se métamorphosent en copépodites en passant rapidement le stade copépodites jeunes (voir page précédente, COKER 1933).

Au temps de la débacle (9.5.1948, 12.5.1950) il y a en plus des nauplii et des copépodites âgés, de nombreux copépodites jeunes. Contrairement au développement de la population des *Diatomus*, le nombre de copépodites jeunes se multiplie et le nombre de copépodites âgés et de nauplii diminue (voir Graph. 15 et 16). Les nauplii de l'hiver sont remplacés par des copépodites jeunes et les copépodites âgés de l'hiver sont remplacés par des adultes au printemps. Dans les épreuves de Juin, les femelles portent des oeufs.

En Juillet, les copépodites jeunes sont remplacés par des copépodites âgés. Le nombre de nauplii se multiplie: ce sont les descendants des adultes de Juin. En Juillet, il y a aussi des adultes, mais la courbe traverse un minimum et les femelles n'ont pas d'oeufs. Ainsi, il existe deux fractions dans la population des Cyclopes.

Une fraction commençant avec les nauplii vers la fin de l'hiver, les animaux arrivant à leur maturation sexuelle en Août (les nauplii de l'automne sont probablement leurs descendants) et une autre fraction où les animaux passent l'hiver comme copépodites âgés ou deviennent copépodites âgés pendant l'hiver, arrivant à leur maturation sexuelle au printemps, leurs descendants existants comme nauplii pendant l'été. Vers la fin de l'été, ces nauplii se transforment partiellement en copépodites jeunes, ils sont probablement représentés par les copépodites âgés dans les épreuves d'automne.

OLOFSSON (1918) a interprété le cycle annuel des *Cyclops strenuus* d'une manière conforme à celle présentée ici. Selon lui, il y a par an, au Spitsberg, une seule génération de *Cyclops strenuus*. Les animaux apparaissent au temps de la débacle comme nauplii ou comme adultes.

Ottsjön. Variation entre les années différentes. — En comparant les épreuves prises immédiatement après la débacle, à des années

différentes, (9.5.1948 et 12.5.1950) on trouve une inégalité parallèle à celle décrite pour les *Diaptomus*. L'eau des épreuves de 1948 étant un peu plus froide que celle des épreuves de 1950, les épreuves de 1948 ont une composition qui se rapproche davantage de la composition des épreuves d'hiver.

La composition du 5.6.1946, est difficile à interpréter parce que les chiffres représentés dans le graphique 15 sont des chiffres de minimum (il y a quelques animaux non classifiés. — voir tableaux 9—10). Cependant on peut dire que la population des épreuves du 5.6.1946 est au moins aussi avancée que celle des épreuves prises à la date correspondante, dans le calendrier, en 1950. Cela veut dire que les animaux de la population de 1946 ont passé leur ontogénèse plus rapidement que ceux de la population de 1950 puisqu'il n'y a qu'une semaine entre la débacle de 1946 et le 5.6.1946. Evidemment cette discussion n'est valide que si l'on présume que le développement de la population *Cyclops* est la même autour de la débacle pour des années différentes. Quoiqu'il en soit, il est évident que le développement n'est pas lié d'une façon absolue aux dates du calendrier.

En examinant les épreuves de l'été on est un peu surpris de constater que les épreuves du 24.8.1948 manquent de copépodites jeunes alors qu'ils sont déjà développés le 22.8.1950. L'été de 1948 semble aussi chaud que l'été de 1950 si l'on en juge à la température de l'eau. Peut-on alors supposer que la différence en composition des épreuves autour de la débacle discutées plus haut ait un effet qui dure jusqu'en Août? L'été de 1951 au contraire était en retard si on compare la température du lac avec les températures de 1948 et de 1950. La débacle arriva fin Mai et les courbes de température en Août montrent assez clairement le retard de la chaleur. Les compositions des épreuves des 11.8. et 20.8.1951, s'harmonisent avec ce retardement, car les copépodites âgés ne sont pas encore disparus, quoique leur nombre va en décroissant du 11.8. au 20.8. On peut également affirmer un retardement des courbes du nombre des Cyclopes adultes en Août 1951.

Les autres lacs. — Le rythme annuel des *Cyclops*, dans les épreuves plus clairsemées de Hottön et de Ånn, n'est discuté que pour rechercher les hypothèses complémentaires, nécessaires pour comprendre la conformité de ce rythme avec les faits obtenus dans Ottsjön.

Les faits obtenus dans Ånn correspondent au rythme des Cyclopes dans Ottsjön. On peut seulement remarquer qu'au printemps de 1948, la métamorphose des nauplii en copépodites jeunes sembla venir plus tôt dans Ånn, quoique la débacle vienne un peu plus tard et que la température soit un peu plus basse le 8.5. que dans Ottsjön le 9.5.1948. Vers la fin Août, la métamorphose des nauplii en copépodites jeunes arrive sans doute plus tôt dans Ånn que dans Ottsjön et la température dans Ånn est ici un peu plus élevée que dans Ottsjön.

Le 31.3.1946, il y a des copépodites jeunes dans Ånn, près du fond où l'eau est la plus chaude, chose sans correspondance dans Ottsjön. Peut-être que cela aussi indique que le cycle annuel vient un peu plus tôt dans Ånn que dans Ottsjön. Cependant il faut remarquer qu'en 1946, dans Ånn, les épreuves ne sont pas prises dans le même bassin du lac que celles prises en 1948.

Les *Cyclops* dans Hottön sont surtout représentés, en hiver, par des nauplii qui deviendraient copépodites au printemps et adultes en été. Si on présume que la fraction qui existe comme copépodites âgés pendant l'hiver et nauplii en Août est une fraction mal développée, on peut prétendre que les faits obtenus dans ce lac vont bien au rythme annuel des Cyclopes dans Ottsjön. Les migrations diurnes des Cyclopes étant moins marquées, l'existence d'un hypolimnium dans Hottön n'a pas le même effet sur le développement des *Cyclops* que sur celui des *Diaptomus*.

Les deux fractions de la population *Cyclops* sont-elles séparées l'une de l'autre et peut-on attendre qu'une telle répartition ait provoqué une différence héréditaire entre les deux fractions? L'auteur regarde cela comme peu probable parce qu'il y a toujours des individus qui se sont développés plus tôt ou plus tard et qui peuvent combattre la séparation. En outre les adultes de Juin peuvent en partie survivre jusqu'en Août et avoir une nouvelle période de propagation en même temps que celle de l'autre fraction. Plusieurs auteurs: LOWNDES (1929), GURNEY (1929) et COKER (1934) ont discuté le polymorphisme dans les espèces de Cyclopes mais ils ne semblent pas regarder les formes comme des formes héréditaires différentes.

La répartition aux différentes profondeurs. La migration diurne.

Selon plusieurs auteurs (HUITFELDT KAAS 1906, SOUTHERN GARDINER 1932, FINDENEGG 1943, PENNAK 1944) les migrations diurnes des *Cyclops* sont beaucoup moins marquées que celles des *Diaptomus*. Quelques exemples illustreront la capriciosité de la migration diurne des Cyclopes. Ils peuvent aussi servir à illustrer la connaissance incomplète des facteurs qui déterminent la répartition des Cyclopes.

Toutes les formes de Cyclopes qui existent dans les épreuves d'hiver, semblent avoir préféré la région au dessous de 5 ou de 10 mètres. Il est très improbable que la migration diurne soit la plus complète pendant l'hiver quand la glace et la neige rendent l'eau particulièrement obscure. Au contraire RUTTNER (1909, 1914) a montré que le plancton a une tendance à se rassembler très près au dessous de la glace les jours où elle est couverte de neige, chose comparable à la migration vers la surface quand la lumière diminue pendant les nuits d'été. Dans les épreuves actuelles peut-être que les animaux

cherchent l'eau plus chaude dans les régions plus profondes, mais pourquoi les copépodites âgés sont-ils rassemblés près de la surface dans Ånn le 31.3.1946? Si les copépodites et les adultes ont une tendance à chercher l'eau chaude, tendance qui est plus forte que la tendance à s'éloigner des régions claires, le jour, (EKMAN 1907 et RUTTNER 1930 ont montré que les Cyclopes se rassemblent dans les couches supérieures, chaude, le jour, pendant le printemps), on peut aussi comprendre pourquoi ces formes sont trouvées dans les épreuves des régions plus hautes de Ottsjön le 5.6.1946, de Hottön, le 10.5.1948. Mais pourquoi les copépodites ont-ils cherché l'eau froide à 15 mètres, dans Hottön, le 2.6.1946?

On pourrait ainsi examiner toutes les épreuves et trouver plusieurs cas où la répartition ne peut pas être expliquée seulement comme l'effet d'une migration diurne simple, sous l'action du vent et de la température de l'eau. Les exceptions peuvent être l'effet du hasard mais aussi de plusieurs facteurs; facteurs qui peuvent influencer sur la répartition des Cyclopes. Il est vide de sens de chercher maintenant une combinaison des facteurs pouvant expliquer la répartition dans les épreuves prises.

On peut souligner comme résultat de l'analyse, dans le Ch. IV, qu'il existe peut-être une migration diurne faible des adultes. Les Cyclopes mâles sont de temps en temps trouvés dans la couche près du fond (Ottsjön le 24.8.48, 23.7. et 17.8.1950, Gesten et Håckren 1951. RUTTNER (1930 page 276), SOUTHERN GARDNER (1932) et FINDENEGG (1943) ont montré la même chose. FINDENEGG a montré que ce fait dépend des migrations diurnes plus marquées pour les Cyclopes mâles.

Il n'y a aucune raison, avec le matériel présent d'objecter les faits obtenus par PLEW PENNAK (1949) et RUTTNER (1943) qui ont démontré qu'il y a une très faible migration diurne de nauplii.

L'effet du vent est montré dans le chapitre IV. Le vent a un tel effet sur la répartition des Cyclopes que chaque tendance à la diversité dans leur répartition, depuis la surface jusqu'à 10 mètres de profondeur, est combattu. L'analyse est limitée à la région entre la surface et 10 mètres de profondeur parce que l'action du vent doit être la plus forte dans les régions les moins profondes.

L'inégalité de la répartition pendant les jours plus calmes comporte une pauvreté dans les épreuves les plus près de la surface pour les nauplii, les copépodites et les adultes pendant l'été et aussi une pauvreté près du fond pour les adultes (en Août). La pauvreté près du fond est un fait qu'on ne doit pas probablement généraliser.

Les nauplii s'assemblent essentiellement dans l'eau profonde, c'est à dire dans la région la plus chaude en hiver et dans la région la plus froide en été.

VII. Cladocères

Le cycle annuel des Daphnies

Pendant l'hiver il y a quelques rares exemplaires de Daphnies.

Au temps qui suit la débacle apparaissent des Daphnies jeunes et des femelles portant des oeufs dans leur chambre incubatrice mais ces femelles apparaissent rarement au début de cette période. Elles sont sans doute toutes écloses des oeufs durables. L'éclosion des oeufs durables ne se produit probablement pas simultanément. La floraison des Daphnies commence sérieusement pendant le mois de Juin. Déjà au mois de Mai on observe quelques exemplaires jeunes avec une petite épine à la carène, mais la plupart sont sans épines. Au début de l'été les proportions sont interverties. En Juillet les quelques rares individus sans épines qui se trouvent mêlés aux autres, sont de vieux exemplaires.

Les Daphnies mâles apparaissent en tant que jeunes, en Juillet et deviennent adultes principalement en Août. Pendant ce mois, on observe les premières éhippies dans la chambre incubatrice des femelles. La densité de Daphnies la plus importante se rencontre pendant Juillet et Août, mais encore au mois d'Octobre, à une température de 3 à 5 degrés (Hottön, 25.10.1948) la pauvreté en Daphnies des mois d'hiver n'est pas encore atteinte; même au dessous de la glace dans Håckren le 18.12.1951 (épreuves avec filet) les Daphnies sont relativement fréquentes.

Classification. — Les Daphnies sont classifiées selon les différentes phases de l'onthogénèse, surtout selon leur longueur. Dans les tableaux elles sont classifiées en deux groupes de longueur. En élaboration primaire la longueur a été plus précisément notée. L'estimation de la longueur était faite en comparant les animaux avec les carrés dont était pourvu la lame de verre du microscope. Le côté d'un carré est de 2 mm.

Dans la classe »femelles adultes» sont compris les individus femelles qui ont atteint la longueur des plus petites femelles portant des oeufs dans leur chambre incubatrice. La classe adulte est ainsi un peu plus vaste et contient aussi quelques animaux qui ne sont pas arrivés à maturation sexuelle. La longueur des femelles portant des oeufs varie pour les lacs différents. En général cette longueur dépasse 1 mm 5, l'épine postérieure de la carapace et l'épine de la carène n'étant pas comptées.

Une autre classe contient les femelles jeunes et les mâles. Souvent les mâles, que on peut séparer sont mis dans une classe speciale mais les mâles les plus jeunes ne sont jamais séparés des femelles jeunes. Dans la classe »Daphnies Jeunes», les plus courtes ont le dos droit et l'épine postérieure concave en arrière à direction dorsocaudale. Les individus trouvés dans Ånn, au fond

du lac, le 16.8.1946, et qui ont inspiré l'étude de la répartition des différentes formes (rens. pré-l. 1948) étaient de ce type, ressemblant aux *neonatae* (selon WOLTEREC 1921).

Le cycle annuel des Bosmines

La floraison des Bosmines commence plus tôt et aussi plus simultanément que celle des Daphnies. Déjà le 12.5.1950, en Ottsjön, immédiatement après la débacle, presque tous les exemplaires de *Bosmina* portent des oeufs dans leur chambre incubatrice.

RUTTNER (1930) a montré que les Bosmines ont deux périodes de propagation par an dans le Lunzer Untersee. SOUTHERN GARDINER (1926) ont montré que les Bosmines dans le Lough Dergh ont complètement disparu pendant une période de l'été. Avec le matériel actuel on peut constater deux périodes de propagation: Après l'épreuve de Ottsjön le 12.5.1950, citée plus haut, les individus portant des oeufs ou des embryons deviennent successivement plus rares pendant Juin et en Juillet 1950 tous les Bosmines observées manquent d'oeufs ou d'embryons dans leur chambre incubatrice. Pendant Août apparaissent des femelles portant des oeufs ou des embryons mais elles ne sont relativement pas aussi nombreuses qu'en Mai. Cette situation se maintient pendant l'automne. Les mâles sont observés pendant Août et l'automne, mais ils sont toujours rares. Le 18 et 19.12.1951 dans Håckren et Ottsjön il y a encore plusieurs Bosmines au dessous de la glace (épreuves prises avec filet). Contrairement aux résultats obtenus par SOUTHERN GARDINER, les Bosmines ne sont jamais disparues d'aucune série d'épreuves prises en eau libre. Dans les renseignements préliminaires on constate un minimum de Bosmines en Ottsjön pendant Août. Les épreuves étaient à cette époque insuffisantes. Dans les investigations suivantes les renseignements préliminaires ne contredisent pas un tel minimum, quoique le nombre de Bosmines semble diminuer vers Août, mais il n'a pas été pris d'épreuves en automne. De plus le cycle annuel des Bosmines dans Hottön montre une augmentation de Bosmines vers Août; peut-être est-ce un retardement du cycle, mais la discussion doit attendre car le matériel pris ne suffit pas.

La répartition aux différentes profondeurs. La migration diurne

Après avoir observé le rassemblement des Daphnies courtes dans Änn, le 16.8.1946, et celui des Daphnies dans Hottön, dans le thermocline, (1946 et 1947), on analysa la répartition des Daphnies dans Hottön (Aout 1948), Ottsjön (12.7.1946, 17.8.1946 et 24.8.1948). La conclusion dans les renseignements préliminaires montre que les Daphnies (surtout les courtes dans Hottön) cherchent à s'éloigner de la surface à cause de la lumière du jour et que dans Hottön, elles sont plus ou moins arrêtées par l'eau froide, plus visqueuse,

mais qu'elles poursuivent leur migration jusqu'aux couches les plus profondes dans les lacs qui manquent de thermocline (à cette époque les Daphnies n'ont pas été classifiées en courtes et longues dans ces lacs).

Quelque soit l'opinion que l'on puisse avoir sur le rapport qui existe entre la cyclomorphose des Cladocères et la viscosité de l'eau, (WESENBERG-LUND, 1926, OSTWALD 1902, Woltereck 1928 b, WAGLER 1927, BERG 1934, 1936, COKER (1939), LIEDER 1950), on ne peut nier l'importance de la viscosité de l'eau sur les mouvements des Cladocères et leur possibilité à flotter. Cette théorie connue et reconnue par plusieurs auteurs, a été prise comme point de départ pour la discussion dans les renseignements préliminaires et s'y est révélée d'une grande probabilité. Dans le travail présent, l'analyse du nouveau matériel peut servir de preuve statistique, parce qu'après l'analyse des renseignements préliminaires la théorie n'est plus une hypothèse choisie au hasard entre plusieurs hypothèses possibles.

Le traitement statistique dans le chapitre IV a relevé que les Daphnies femelles au stade de la croissance et les mâles étaient rassemblés aux environs du thermocline, le jour, dans Hottön et Håckren, mais près du fond dans Ottsjön. Pourtant il faut remarquer que le rassemblement des Daphnies dans une des trois stations dans Hottön le 23.8.1950, était un peu en dessus du thermocline et que le rassemblement des Daphnies près du fond dans Ottsjön était très évident pour certaines séries mais manquait complètement dans d'autres séries. Cela ne ressort pas de l'analyse statistique parce que cette analyse est et doit être le développement aveugle d'une hypothèse.

La liaison entre le rassemblement des Daphnies et le thermocline dans les deux lacs où le thermocline existait à des profondeurs différentes est une forte et claire affirmation qu'il existe une véritable liaison.

Les Bosmines ne sont pas classifiées selon leur longueur. Il y a un maximum de Bosmines aussi dans le thermocline de Hottön et Håckren et près du fond dans Ottsjön pendant le jour.

Souvent les auteurs précédents ont constaté que les Daphnies ne sont pas influencées par la température dans leurs migrations diurnes parce que les animaux passent à travers le thermocline. Mais FINDENEGG (1943) a montré que les *Daphnia cucullata* vivent substantiellement au dessus du thermocline, préférant l'eau chaude, et, KIKUCHI (1930) et FINDENEGG (1943) ont montré que la *Daphnia longispina* vit en dessous du thermocline, cherchant l'eau plus froide. Ces différentes réactions sont probablement l'expression des différentes prétentions des Daphnies.

Ces constatations ne sont pas opposées aux conclusions en ce qui concerne l'influence de la viscosité discutée plus haut pour les lacs du Jämtland. Naturellement dans les autres lacs les réactions des Cladocères vis à vis de la température ou de la lumière peuvent être telles que, l'effet de la

viscosité en est masquée, où bien l'effet des variations de la viscosité peut être insignifiant en regard des mouvements propres aux planctons.

On pourrait supposer que le rapport entre la viscosité et la répartition des planctons est d'un déterminisme apparent mais faux en réalité, parce que les deux phénomènes pourraient être dirigés par un autre facteur, facteur qui se modifierait brusquement dans le thermocline. Les faits dont on a rendu compte dans le chapitre III peuvent fournir quelques indications au lecteur qui veut chercher parmi les autres facteurs.

Si on cherche une relation entre la température et le rassemblement des Cladocères dans le thermocline ou près du fond, on affronte plusieurs difficultés. Par exemple: la température de toutes les régions de Ottsjön (lac sans thermocline) est souvent plus basse que la température aux régions du thermocline dans Hottön où le rassemblement des Cladocères se produit. Peut-être que la rapidité de la baisse de température dans le thermocline peut retarder les Cladocères dans leur descente pendant la migration diurne.

Les épreuves dans Hottön et Håckren sont prises seulement par jours calmes, mais les épreuves dans Ottsjön sont prises par jours calmes et par jours venteux. Il y a des rassemblements près du fond dans ces deux types de jours. En conséquence ce n'est pas une fuite des régions remuées par le vent.

Il faut exclure la possibilité que le thermocline et le fond du lac coïncideraient avec un certain état d'obscurité, état d'obscurité qui serait recherché par les Daphnies et les Bosmines pendant leur migration diurne. Le tableau 1 donne des valeurs de transparence. On peut voir qu'il n'y a pas de rapport évident entre la transparence et la répartition des Cladocères dans les différents lacs.

Dans le chapitre IV on a prouvé que les Daphnies femelles adultes se rassembleraient, le jour, dans les couches supérieures. Le même phénomène a été discuté dans les renseignements préliminaires, mais il n'y a aucune hypothèse quant à la position exacte de ce rassemblement. Cependant on a examiné la répartition aux différentes profondeurs. Il y a un maximum à deux mètres. Les Daphnies et Bosmines évitent la surface.

En ce qui concerne les migrations différentes des Daphnies femelles adultes et les formes de croissance, il y a des travaux dont les conclusions disent exactement le contraire de celles émises ici. Les adultes se rassembleraient, pendant le jour, plus profondément que les jeunes. Mais il y a des travaux dont les conclusions concordent exactement avec celles présentées ici. SOUTHERN GARDINER (1932) ont déjà rendu compte d'un cas concordant avec la répartition des Daphnies dans le Jämtland. En Loc Dergue il y a un rassemblement de Daphnies adultes entre deux mètres et la surface, le midi. Ils ne pouvaient donner une position plus précise à cause de la méthode

employée. Les jeunes s'éloignaient plus loin de la surface, le jour. Ils ont cependant montré que les migrations des adultes se produisent à l'aube, ceux-ci descendant vers le fond et remontant bientôt vers la surface. WORTHINGTON (1931) a aussi rendu compte d'un cas, dans le lac de Lucerne, où les jeunes se rassemblaient le jour plus profondément que les adultes. SOUTHERN GARDINER (1932) citent et discutent plusieurs conclusions données par d'autres auteurs et qui s'opposent aux leurs et à celles du présent travail.

Il n'y a aucune raison de nier la validité des résultats différents. Les migrations des Daphnies sont certainement diverses pour différents milieux et pour différentes espèces.

L'auteur ne veut proposer aucune hypothèse pour éclaircir le fait qu'en général les Daphnies adultes demeurent près de la surface, même le jour.

VIII. Autres planctons

Dans ce chapitre il faut spécialement rappeler les résultats de VANDEL (1919) et de VIVIÉR (1937), à savoir que les grandes formes planctoniques peuvent éviter les engins de capture de leur propre mouvement et les épreuves sont en conséquence déficientes à leur égard. Il faut aussi se rappeler que la grandeur des mailles dans les filtres employés sont de 70—90 μ ce qui raréfie aussi dans les épreuves la présence des rotifères et naturellement de phytoplancton.

Zooplancton: Crustacés

Hétérocope saliens. LILLJEBORG. — En dehors des épreuves prises dans une crique peu profonde (station X dans Ottsjön) où on trouve déjà des Hétérocopes adultes le 4.7.1950, les Hétérocopes adultes ne se rencontrent pas dans les épreuves avant Août. Des copépodites de cette espèce sont trouvés en Juillet. En Automne les Hétérocopes ont disparu. Les Hétérocopes sont trouvés spécialement dans les couches supérieures des lacs comme HUITFELDT KAAS (1906) l'a déjà constaté.

Holopedium gibberum. ZADDACH. — Deux exemplaires isolés sont obtenus dans Ånn, le 31.3.1946, mais ordinairement l'*Holopedium* apparaît au commencement de Juin. Des femelles portant des oeufs ou embryons dans leur chambre incubatrice ne sont pas observées avant Juillet. Après Août l'*Holopedium* devient rare.

Sida crystalina. MÜLLER. — Deux exemplaires ont été obtenus (voir tableau 10).

Chydoridae. — 23 exemplaires ont été obtenus avec le chercheur. Ils ne sont pas classifiés en genre.

Polyphemus pediculus. (LINNÉ). — *Polyphemus* appartient avant tout aux régions peu profondes voisinant les rives, comme le dit HUITFELDT KAAS

(1906), mais est aussi trouvé au dessus des grandes profondeurs dans le bassin central de Hottön (25.8.48). *Polyphemus* est obtenu dès Juillet mais dans ces épreuves il y a des spécimens portant des oeufs dans leur chambre incubatrice et en conséquence les premiers *Polyphemus* de l'année sont éclos plus tôt, peut être en Juin. Pendant l'Automme *Polyphemus* est disparu.

Bytotrephes longimanus. LEYDIG. — *Bytotrephes* est observé en Juillet et Août, mais en Août ont été trouvés des femelles portant des oeufs.

Dans le tableau 10 tous les exemplaires des genres cités ci-dessus sont juxtaposés. On peut voir qu'ils n'ont été obtenus qu'en été — quelques *Holopedium* mis à part. Ils sont aussi reconnus comme apparaissant à la saison chaude.

Zooplancton: Rotifères

Parmi les Rotifères, les *Notholca longispina* KELLICOT et les *Conochilus* sp. sont les Rotifères les plus souvent obtenues. Pour illustrer l'abondance des *Notholca* quelques chiffres sont juxtaposés en tableau.

Ottsjön le	9.5.48	12.5.50	10.6.50	15.7.50	17.8.50	24.8.48
\bar{x}	4	4	6	16	5	1
Ånn le	8.5.48	23.8.48				
\bar{x}	0.5	16				
Hottön le	10.5.48	25.8.48	25.10.48			
\bar{x}	3	1.2	0.7			

Les moyennes sont calculées pour chaque série avec toutes les épreuves de la série. Il n'est pas facile de donner une expression quantitative à l'abondance des *Conochilus* parce que les colonies sont souvent déchirées par les méthodes de capture et que l'on obtient souvent des individus isolés.

Dans toutes les épreuves prises avec le chercheur de plancton, les nombres suivants ont été obtenus: 62 *Keratella*, 54 *Ploeosoma*, 60 *Polyarthra*, 220 *Asplanchna*, 37 Rotifères non classifiées. Les Rotifères sont notées en élaborant les épreuves, mais à cause de l'analyse systématique incomplète on ne donne que ce seul compte rendu.

Phytoplankton

Les Tabellarias sont les Phytoplanktons les plus souvent obtenues. Dans Ottsjön 1948, 1950, 1951 le nombre de Tabellarias alterne généralement entre 10 et 100 individus dans chaque épreuve en eau libre et l'abondance dans les autres lacs est environ de même grandeur. Il y a donc des cas où la moyenne ne dépasse pas 10. Dans Ottsjön 1946 on affronte un autre extrême: moyenne d'environ 350 pour toutes les épreuves en eau libre (épreuves de 10 litres!).

Parmi les autres phytoplanktons dominent les *Zygnemales*, *Anabaena* et un groupe non classifié.

Dans l'ensemble des épreuves on a obtenu: 32 *Micrasterias* sp, 28 *Staurastrum* sp, 52 *Pediastrum* sp et 165 Diatomées — les Tabellarias mis à part. L'hiver le phytoplancton est extrêmement rare dans les épreuves.

Les données concernant le phytoplancton sont évidemment très incomplètes et ne sont introduites ici que pour donner un aperçu du milieu où vit le Zooplancton.

IX. Le Plancton dans les différentes stations d'un même lac. Différences entre les lacs

La question des différences en abondance entre les différentes stations d'un même lac est traitée par SOUTHERN GARDINER (1926), RUTTNER (1930), LANGFORD (1938), RICKER (1938), TONOLLI (1949 b) et autres.

Le chapitre IV montre quelles difficultés il y a pour prouver les différences entre les stations. Ces différences sont indiquées avec une signification * et ** pour *Diatomus* adultes et *Daphnies* de la zone pélagique dans Ottsjön, août 1950. Pour *Cyclopes nauplii* et adultes, Ottsjön, zone pélagique, août 1950 et *Cyclopes nauplii* et copépodites, Ånn, mai 1948, station près du bord de la glace fondante et station en eau libre, ces différences ne sont pas significatives.

On peut à priori s'attendre à des différences d'abondance de planctons dans les épreuves prises près des rives ou des embouchures (zone littorale) et dans les épreuves prises dans la zone pélagique. Hors il n'y a que quelques espèces qui semblent se rassembler près des rives; par exemple *Polyphemus pediculus* (HUITFELDT KAAS 1906, ainsi que dans le matériel actuel). En outre les *Bosmina coregoni* seraient d'autres exemples de ce phénomène.

Ces espèces mises à part, les régions voisinants les rives sont connues comme des régions pauvres en plancton typique. Ce phénomène est si connu qu'on a construit le concept »fuite des rives» BURCKHARDT 1910, SOUTHERN GARDINER 1926, RUTTNER 1930).

S'il existait une fuite effective des régions peu profondes voisinants les rives ce phénomène pourrait aussi provoquer une pauvreté de planctons dans les fleuves. Mais les auteurs ont des opinions diverses concernant le plancton des fleuves. WOLTEREC (1908) constate que la majorité du plancton ne quitte pas le lac étudié par lui, ni le jour, ni la nuit. Il constate qu'il existe une diminution abrupte de la richesse planctonique dans la région où les courants près de l'issue des eaux peuvent être remarqués. D'autres auteurs (par exemple LIEDER, 1950) ont montré que le zooplancton est emporté par les fleuves. Mais soit que le plancton quitte le lac, soit le contraire, les fleuves sont généralement pauvres en plancton (KOFOID 1903—1908, SOUTHERN GARDINER 1926, REIF 1939). Voir Tableau 9, Ottsjön 15.8.50, R et Håckren 31.7.51, E.

La grande variation du nombre de planctons qui caractérise les épreuves prises près des rives et des embouchures et l'absence d'épreuves de nuit applicables ici mettent dans l'impossibilité avec le matériel présent d'éclaircir tous les problèmes discutés. On peut souligner (le *Polyphemus* et *Bosmina* mis à part) la pauvreté en plancton des épreuves prises près des rives ou des embouchures. Mais cette pauvreté existe aussi le jour, si le vent n'est pas trop fort dans la couche près de la surface de la zone pélagique. Peut être existe-t-il aussi des différences entre ces deux régions mais à cause de leur pauvreté ces différences ne sont pas analysées avec le matériel actuel. Il faut donc dire qu'il existe — en tant qu'exceptions rares — des épreuves prises près des rives avec un plancton extrêmement nombreux, de vrais essaïms. La variance intraclasse est très grande près des rives.

En dehors de différences entre les lacs, déjà discutées: différences du cycle annuel des Copépodes (Ch V—VI), différences de la répartition des Cladocères, le jour (Ch VII), on peut remarquer que les Copépodes atteignent une plus riche floraison dans Ottsjön que dans Hottön mais il y a intervention pour les Cladocères. Le plancton dans Gesten montre avec Ottsjön des ressemblances, mais semble pauvre, probablement parce que son débit est grand comparé à la grandeur de son bassin. Le même phénomène est reconnu par HUITFELDT KAAS 1906. Les courbes de température dans Gesten comparées aux courbes dans Håckren indiquent l'effet nivelant des courants sur la stratification thermique dans Gesten. Gesten peut aussi être plus exposé au vent, mais cela est moins probable. Les courants sont bien connus de ceux qui emploient les routes d'hiver sur la glace ou travaillent avec les trains de bois à travers le Gesten. Håckren a un bassin central de même profondeur environ que le Gesten mais il a une situation mieux protégée des courants qui apparaissent aux endroits de l'apport des affluents ou du déversement de l'émissaire. Le plancton dans Håckren est plus riche que dans Gesten et la composition ressemble à celle dans Hottön — elle est riche en Cladocères.

Summary

The abundance and ecology of *Diatomus laticeps*, *Cyclops scutifer*, *Daphnia longispina hyalina* and *Bosmina coregoni* have been studied by means of a plankton sampler (Photo, p. 73). Data concerning other crustacea, more seldom met with in the lakes investigated, were also collected. The position of the lakes is given on the map, p. 117.

Environment. The environmental conditions can be summed up as follows: uniformity for most parts of the lakes in the physical and chemical conditions (Ch. III), and scarcity of rotifers and phytoplankton — a scarcity which concerns the forms retained by the filters employed (mesh size 70—90 μ ,

Ch. VIII). The nanoplankton has not been studied. The thermal stratification in L. Hottön forms an exception from this uniformity. An epilimnion, a metalimnion and a hypolimnion are to be found in this lake. In Lakes Ottsjön, Gesten, Håckren, Sällsjön and the part of L. Ånn examined, the thermal stratification is counterbalanced by frequent winds and the extensive flow. The importance of the flow is relatively greater in the smaller lakes. The bottom water in these smaller lakes is sometimes colder in summer than the water in the rest of the vertical. For further particulars, see the Graphs 1—14.

Statistics. We can *a priori* expect that the number of plankters of one species, obtained in a plankton sample, belongs to a Poisson distribution. The variance in a Poisson distribution is = the mean. The variates of a Poisson distribution may, however, be examined under certain circumstances by means of the ordinary »analyses of variance» and this has been done in the present paper. The variance for a subgroup in the present material, estimated with the last-mentioned method, is in many cases considerably greater than the mean for the subgroup. No doubt, the subgroups too are complex, with (small) differences in time and place between the samples. Furthermore, deficiencies in the method must be reflected in the »variance within subgroups». It is proposed that the variance within subgroups is often so high that the significance of the differences between plankton abundance in different parts or layers of a lake is underrated.

Distribution of plankton at different depths during daytime. The factors possibly affecting the abundance and distribution of plankton are numerous. Consequently, it is dangerous to pick out a combination of factors which may explain the material obtained in one certain investigation, for in this way a hypothesis *a posteriori* is presented.

In the lakes of Jämtland investigated here the uniformity of the physical and chemical properties simplifies the choice of hypotheses. It is assumed as a hypothesis that the frequent strong winds blowing over L. Ottsjön (Table 2, Graph 6) which exert a mingling effect on the water layers, hinder the zooplankton between the surface and a depth of ten metres in their search for the water layer they prefer. The causal connection between the distribution of the *Cladocera* and the viscosity of the water — a connection, statistically examined for *Daphnia* in a preliminary account (LINDSTRÖM 1949) — is also regarded as a hypothesis. Naturally there are many other premisses, but there is no need for a closer discussion of them as they may be regarded as generally accepted facts.

The distribution of *Diaptomus*, *Cyclops*, *Daphnia* and *Bosmina* at the surface layer and the layers (2 m) 5 m and 10 m below the surface has

been examined by means of a χ^2 test. The test shows that a divergence from a supposed distribution 1: (1:) 1: 1 is more probable on the days with slight wind than it is on the days with strong wind. For most forms the χ^2 does not exceed or only just exceeds a magnitude with the conventional significance of * on the days with strong wind. The reader is referred to pp. 80—81 for particulars concerning the nauplii and older copepodids.

The plankters are consequently concentrated in the layers they prefer on the days with slight wind.

The statistical analysis shows furthermore that:

1. *Cyclops*, *Daphnia* and *Bosmina* avoid the surface on the days with slight wind (L. Ottsjön). »Surface» means 0— $1/2$ m below the real surface.
2. The *Cyclops* nauplii prefer the deep layers (L. Ottsjön).
3. The *Daphnia* males and juveniles are concentrated near the bottom during the days (with or without wind) in thermally unstratified lakes, but are concentrated in the thermocline in stratified lakes.
4. The adult *Daphnia* females are concentrated in the 2 m-depth-layer during days with slight wind.
5. The bulk of the *Bosmina* is found in the same layers as the *Daphnia* males and juveniles. The *Bosmina* is not examined as to different forms in the life cycle.

These facts are in close conformity with the hypotheses that the wind exerts a mingling effect on the upper water layers which impedes the plankters from reaching the water layer they prefer and that the diurnal downward migrations of the *Daphnia* males and juveniles and the bulk of the *Bosmina* are carried out until water layers with greater viscosity are reached or down to the bottom layers in unstratified lakes.

The diurnal migration. A diurnal migration is established for the adult *Diaptomus* but is less evident for the *Cyclops*. *Diaptomus* seems to be most abundant in the surface layer at dusk and not at midnight. These facts are in close conformity with earlier investigations. The existence of a diurnal migration of *Daphnia* and *Bosmina* is not established statistically with the present material. Such a proof cannot be said to be urgently needed, bearing in mind the numerous works on this subject.

The annual cycle. The annual cycle of *Diaptomus* and *Cyclops* is mainly analysed with material from L. Ottsjön. The winter entails a uniform state of development for the *Diaptomus* population i.e. resting eggs (a few nauplii). The *Cyclops* pass the winter as nauplii or as older copepodids.

It may perhaps be necessary to adopt a somewhat more complicated system (p. 102). The essential fact is, however, that the development of the *Cyclops* is retained in winter when they reach the 4th—5th copepodid stage.

COKER (1933) has shown in laboratory that such a retainment is provoked by extremely poor food conditions. Such conditions should occur during the winter in L. Ottsjön.

When the break-up of the ice occurs, a uniform *Diaptomus* population and two fractions of the *Cyclops* population are in existence. The further development during spring and summer is best illustrated by Graphs 15 and 16. In August the *Diaptomus* females carry eggs whereas one *Cyclops* fraction attains sexual maturity in June, the other in August. Only scattered particulars are obtained regarding the copepod populations during the autumn.

The material from the other lakes is not sufficient for a complete analysis but the data obtained indicate that:

1. A second fraction of the *Diaptomus* population is also to be found a fraction which passes the winter as adults.
2. One of the two *Cyclops* fractions may be suppressed.
3. The summer thermal stratification in L. Hottön complicates the picture and exerts a levelling effect on the difference between the two *Diaptomus* fractions, which is to be found during the winter and spring.

An effective genetical isolation is probably not maintained between the two fractions of the *Cyclops* population, nor between the two fractions of the *Diaptomus* population.

The years, during which the investigation was carried out, differ regarding the time for the break-up of the ice and other thermal conditions. The annual cycle of the plankters is retarded during the cold years and accelerated during the warm years. The causality is not completely analysed.

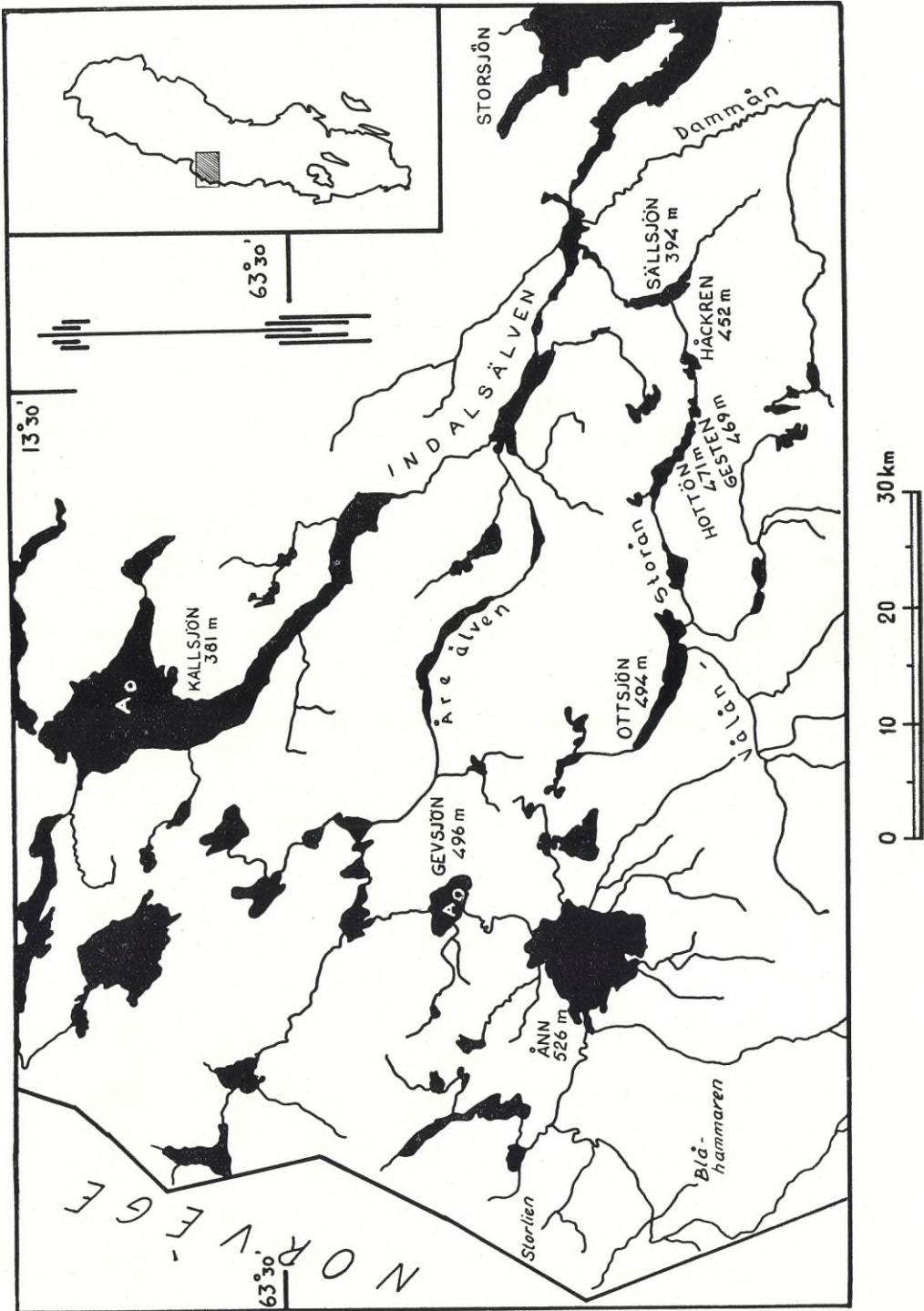
Differences between various stations of a lake and between lakes. In the shore region (0—1—2 m depth) the *Polyphemus* is more abundant than in other parts of the lakes but generally the shore region is about as poor in zooplankton as the surface layer over the pelagial region on days with slight wind. Now and then, however, real swarms of *Bosmina* appear (Tabl. 9, L. Ottsjön, Y, 21.8.50).

It seem as if the plankton is poor in streams, and in lakes, where the flow is great compared with the basin. Possibly the *Cladocera* populations are more sensitive to currents as they are badly developed in lakes, where the mixing effect of winds (L. Ottsjön) or the flow (L. Gesten) is great.

Carte 1. Carte général. A pour Gevsjön et Kallsjön donne les stations de recherches. Les chiffres donnent l'altitude.

General map of region investigated. A at L. Gevsjön and L. Kallsjön indicates stations sampled. Numbers show altitude.

At midsummer the sun sets at 10 p.m. The break-up of the ice usually occurs in May.

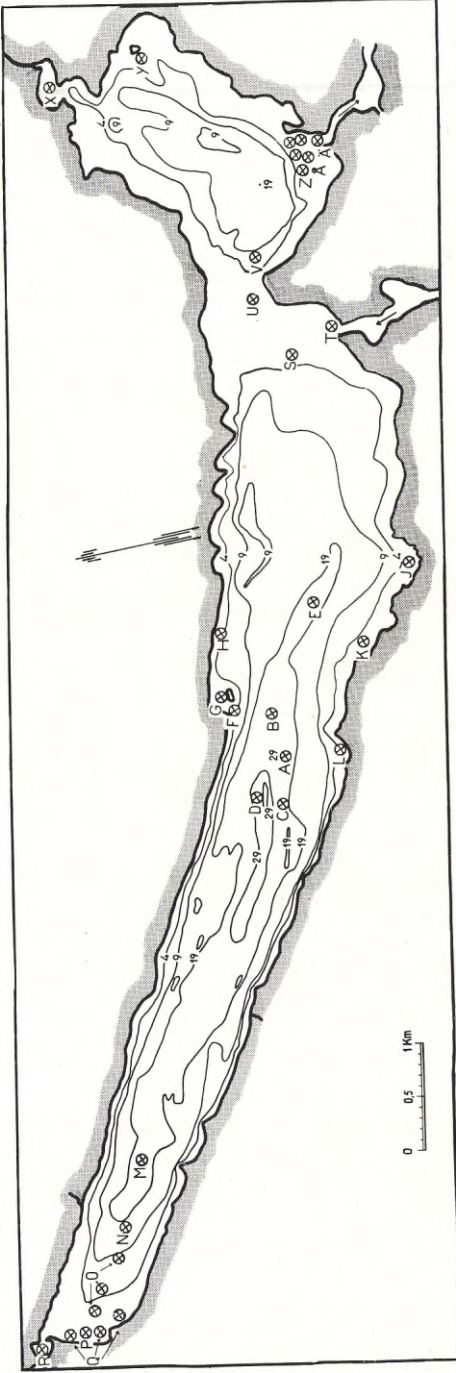


Carte 1.

Carte 2. Carte pour Ann. Les lettres donnent les situations des stations.
Map for Ann. Letters indicate stations.

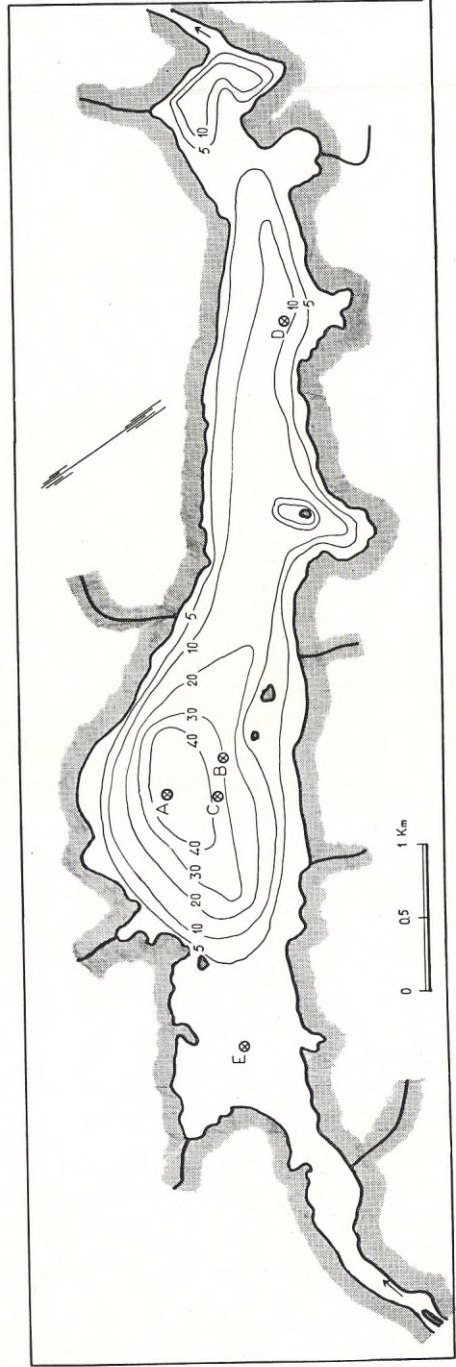


Cartes 3—6. Cartes bathymétriques. Les lettres donnent les situations des stations.
 Bathymetrical maps. Letters indicate stations.

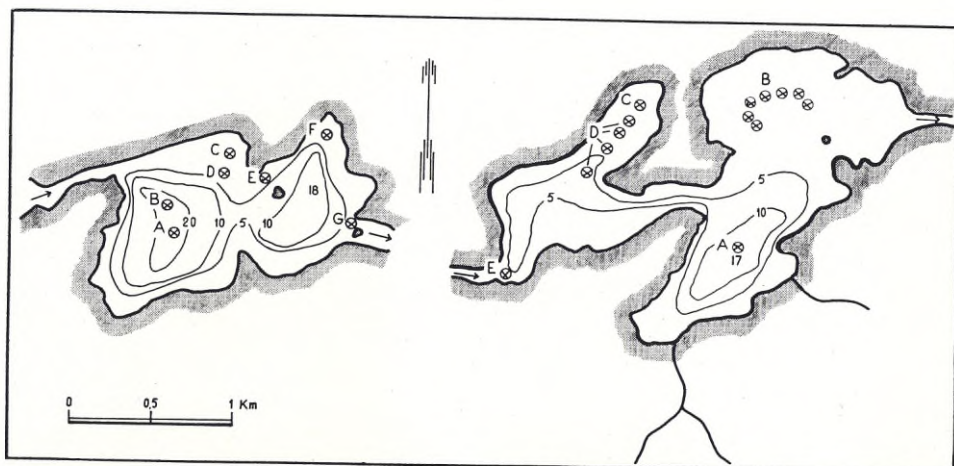


Carte 3. Ottsjön. L'embouchure de l'affluent principal (sud) est près de l'émissaire mais en est séparé par un vaste delta (S—U—V). Les vents soufflent souvent dans le sens de la longueur du lac. Autour de la station B, le fond rocheux, sablonneux et caillouteux descend jusqu'à 17 m de profondeur par endroits.

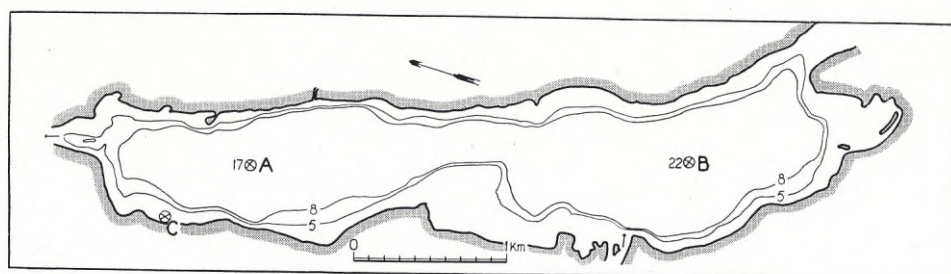
L. Ottsjön. The mouth of the main affluent (south) is not far from the outflow, but separated from this by a big delta (S—U—V). The wind frequently blows along the lake. At Station B the sand-gravel and shingle-rock bottom reaches down to 17 m in certain places.



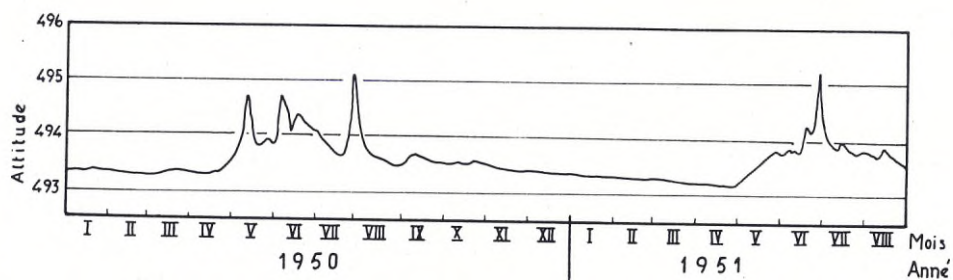
Carte 4. Holtjön.



Carte 5. Gesten (à gauche) et Håckren (à droite).



Carte 6. Sällsjön.

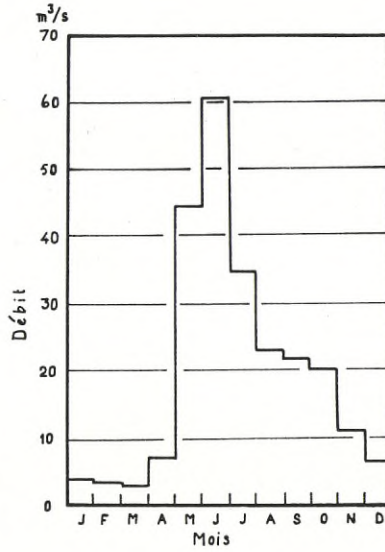


Graphique 1. Variation du niveau pour Ottsjön 1950—1951. On y observe la crue du printemps qui correspond à la fonte des neiges. Selon *Indalsälvens Regleringsförening*.

Level variation at L. Ottsjön 1950—51. It may easily be observed how the snow, stored in the high mountains, is released in the spring.

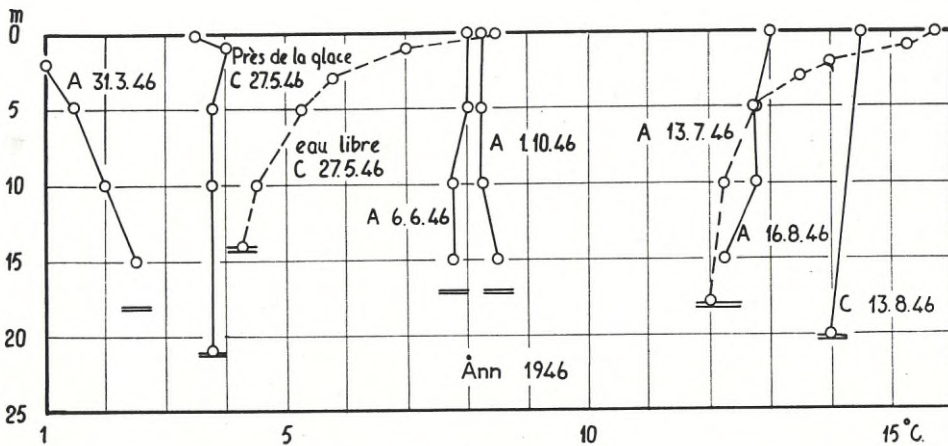
Graphique 2. Débit dans l'émissaire de Ottsjön pour 1909—1947, moyennes mensuelles. Selon *Vattenbyggnadsbyrå*, 28.2. et 30.11.1948.

Flow from L. Ottsjön, monthly averages or 1909—1947.



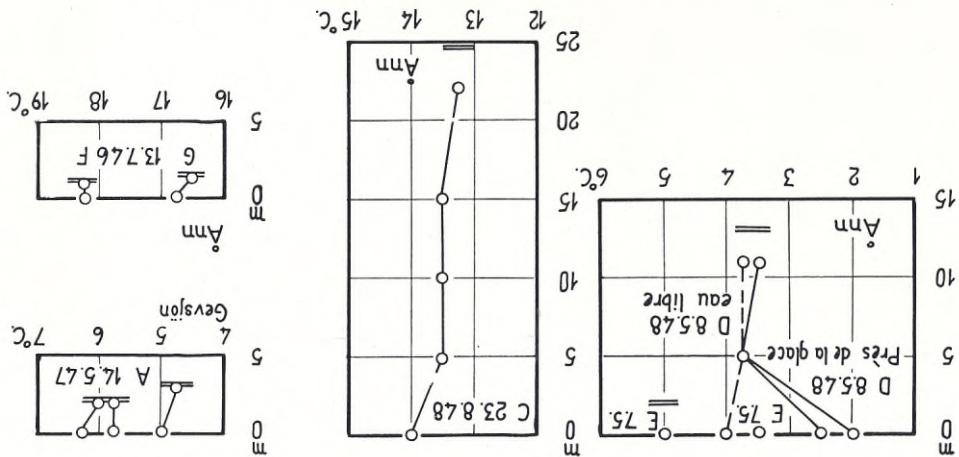
Graphiques 3—14. Lignes de température. Le signe (=) mis sous la plus basse observation de température indique la profondeur totale.

Temperature curves. The sign (=) indicates the total depth.

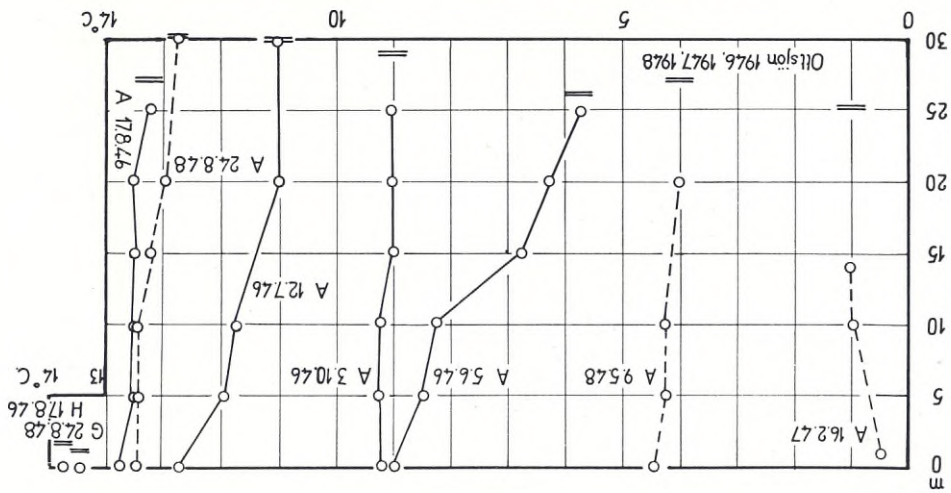


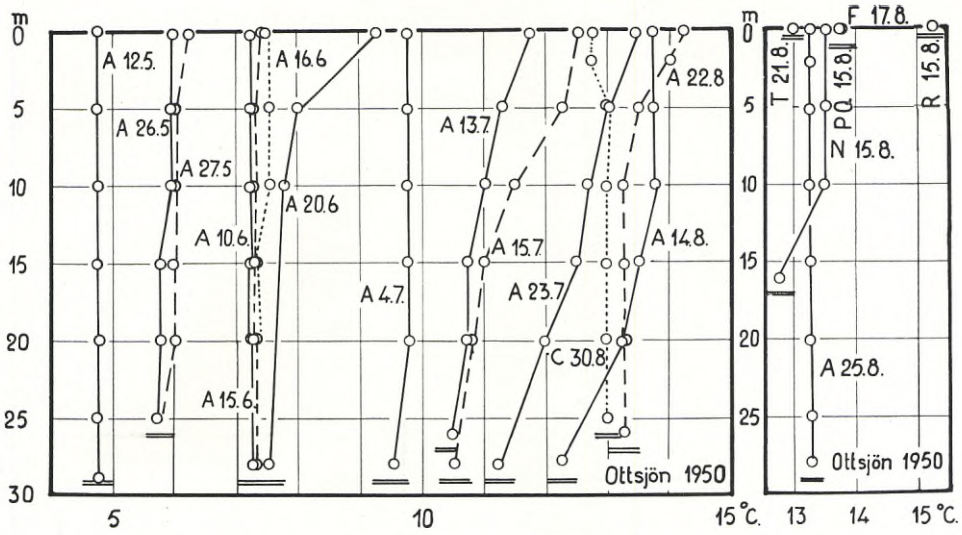
Graphique 3. Température, Ann 1946.

Graphique 4. Température, Ann 1946 et 1948, Gevsjön 1947.



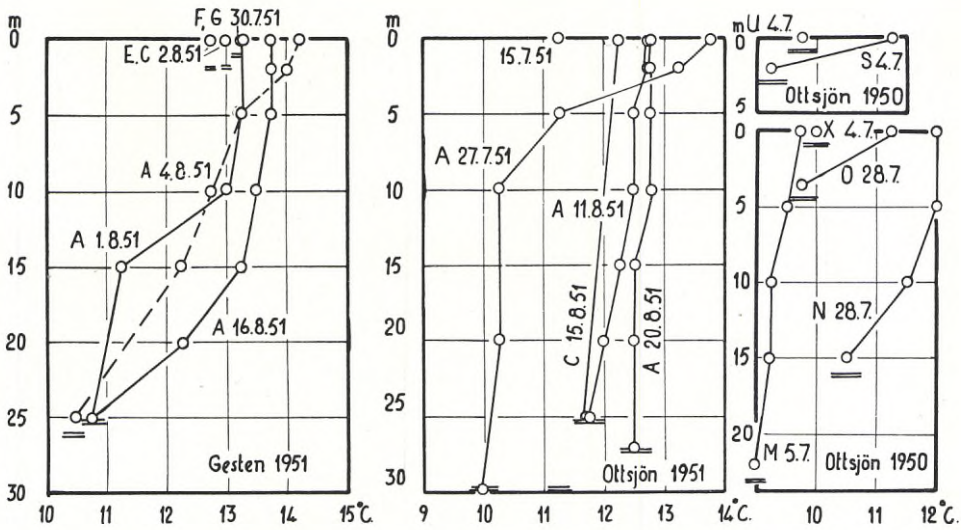
Graphique 5. Température, Ollsjön 1946, 1947 et 1948.



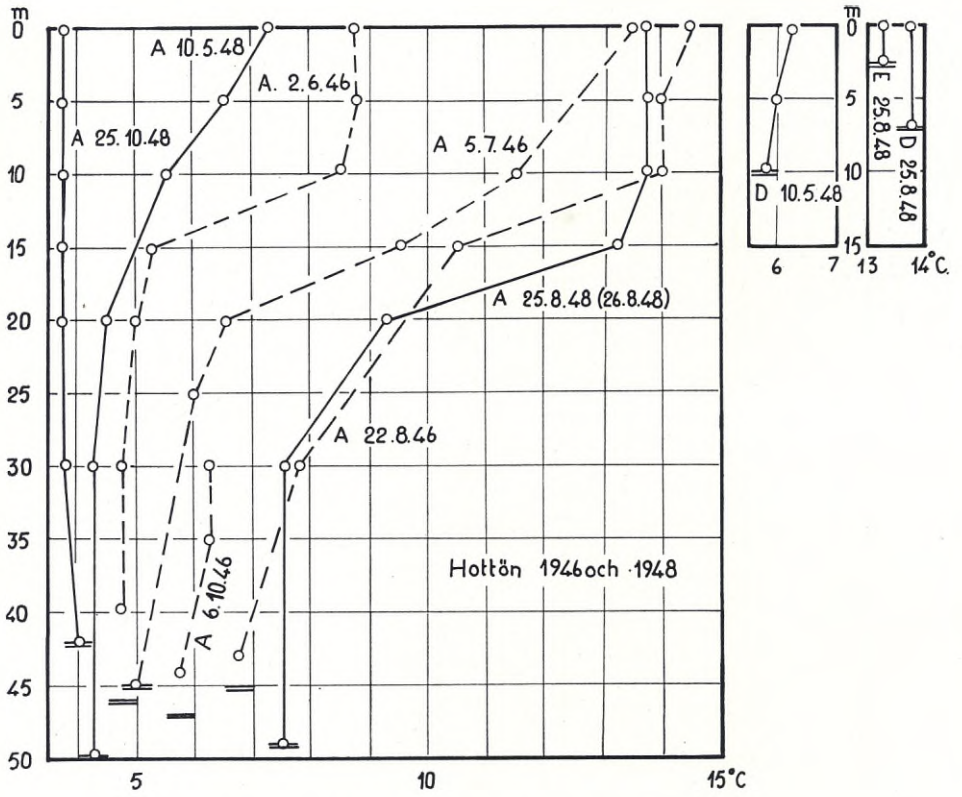


Graphique 6. Température, Ottsjön 1950. Si une stratification thermique commence à se développer elle est bientôt éliminée par des vents forts.

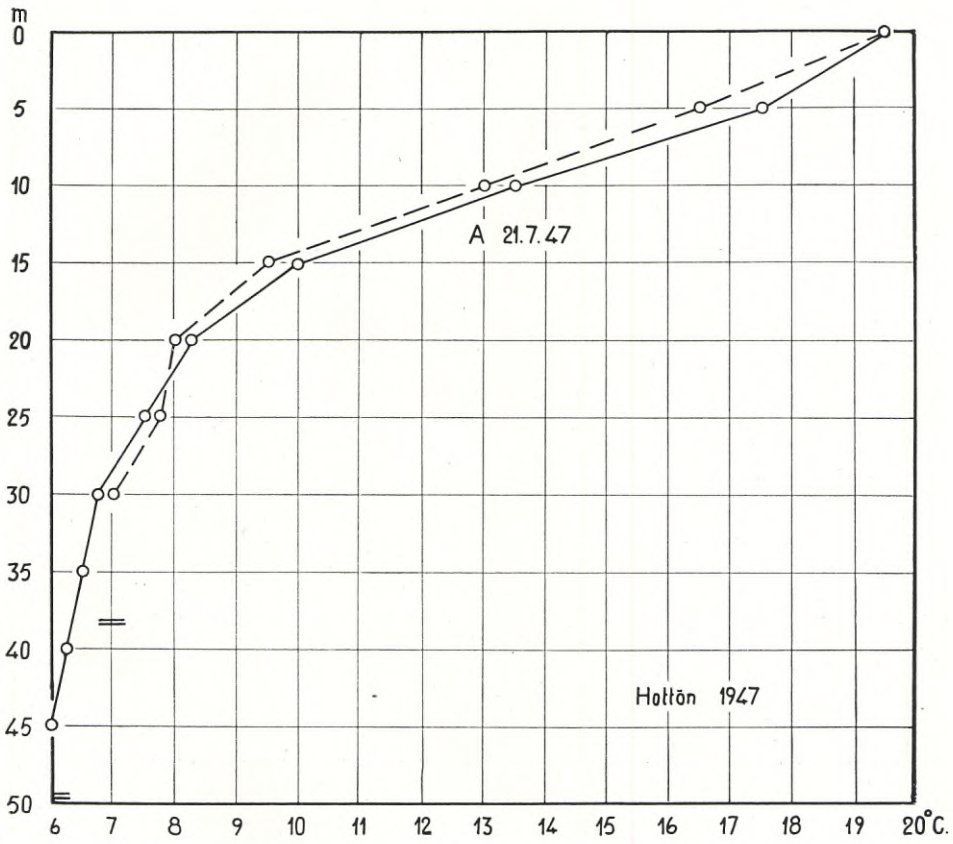
Temperature curves for L. Ottsjön. Every stratification beginning during warm, calm periods is eliminated soon afterwards through strong winds.



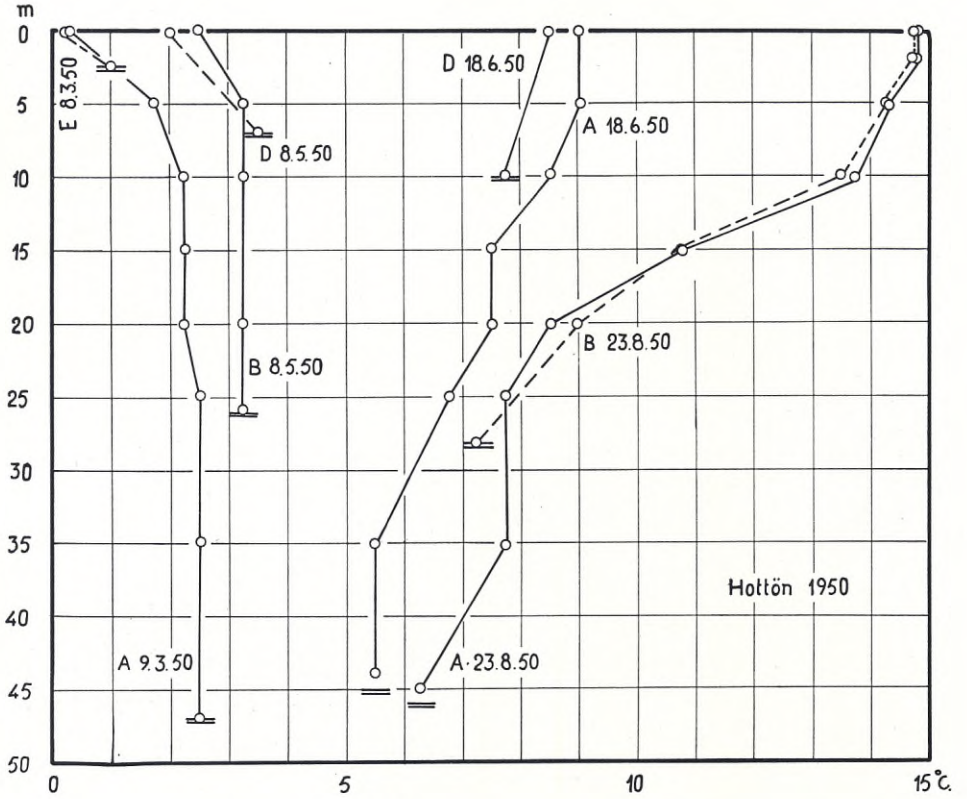
Graphique 7. Température, Ottsjön 1950 et 1951, Gesten 1951.



Graphique 8. Temperature, Hottön 1946 et 1948.



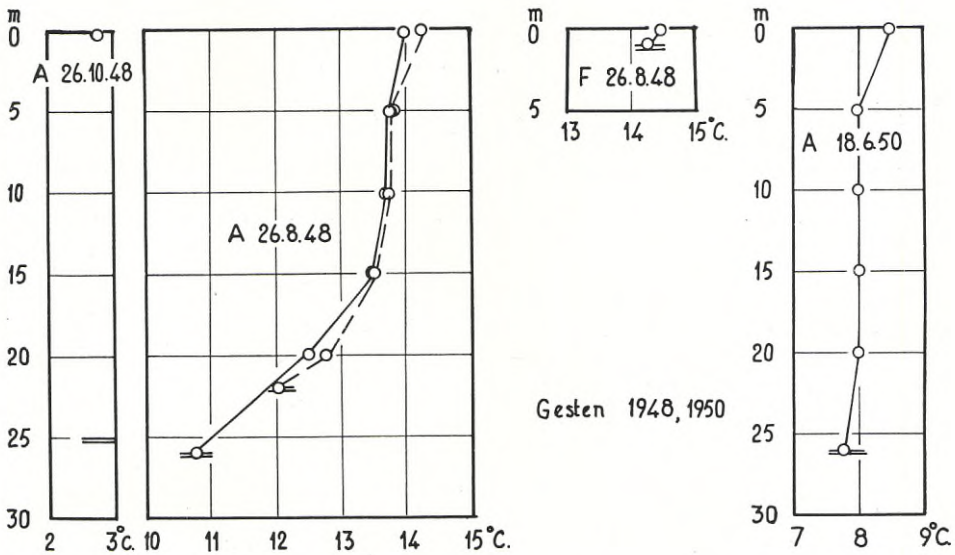
Graphique 9. Temperature, Hottön 1947.



Graphique 10. Température, Hottön 1950.

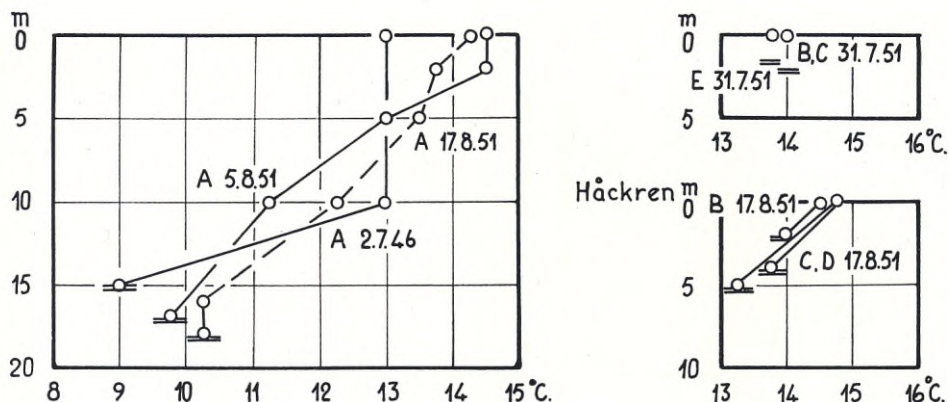


Graphique 11. Température, Gesten 1946.



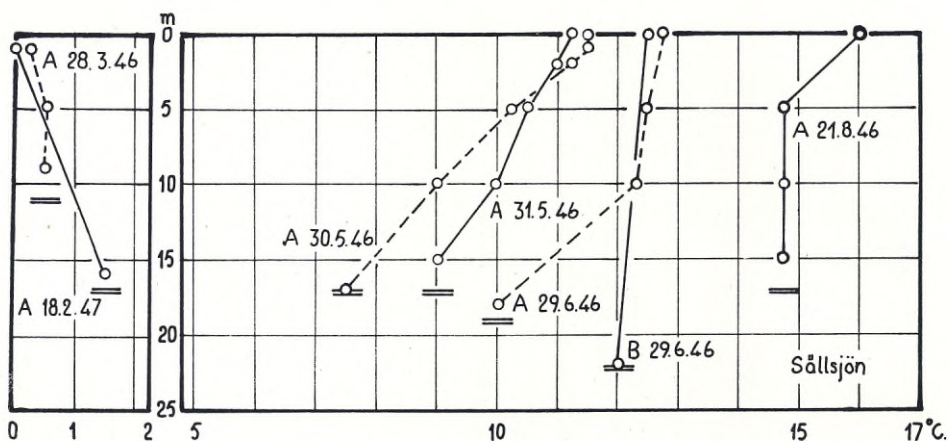
Graphique 12. Température, Gesten 1948 et 1950. Le débit est grand comparé à la grandeur du bassin du lac. Voir aussi graphique 7.

Temperature curves for L. Gesten 1948 and 1950. The flow is considerable compared with the basin of the lake. See also Graph. 7.



Graphique 13. Température, Häckren 1951. Le débit est grand comparé à la grandeur du bassin mais le bassin central est mieux protégé des courants que celui de Gesten.

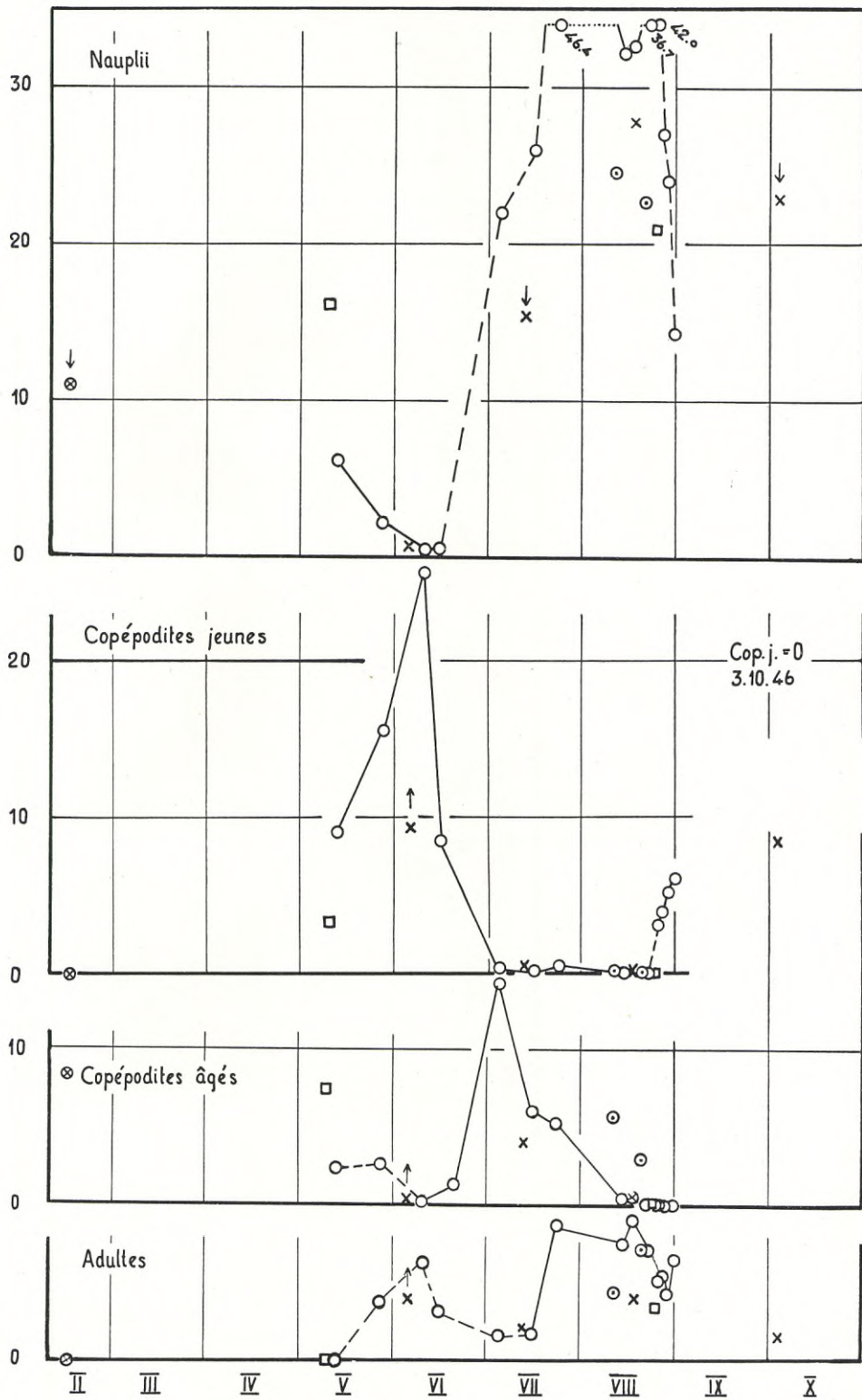
Temperature curves for L. Häckren 1951. The flow is considerable compared with the basin of the lake, but the central basin is better protected against currents than the central basin of L. Gesten.



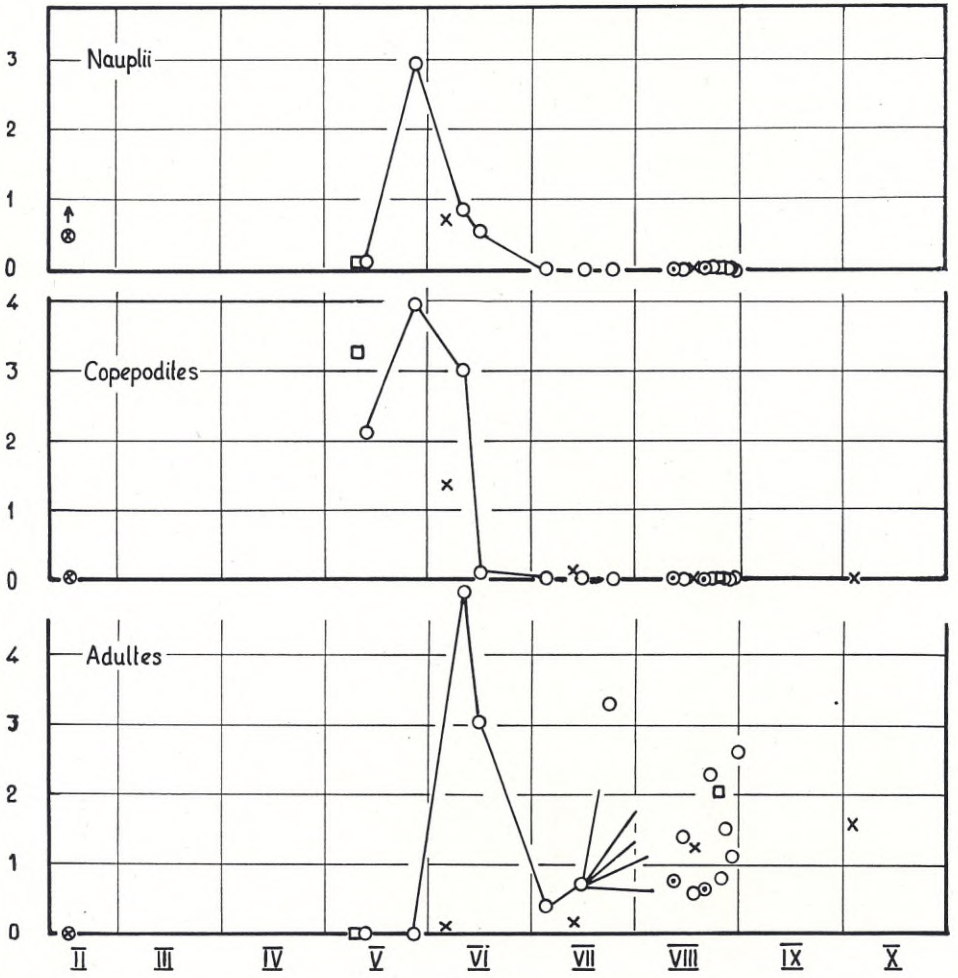
Graphique 14. Température, Sällsjön 1946 et 1947.

Graphique 15. Cycle annuel pour *Cyclops* dans Ottsjön. Les diagrammes 15 et 16 sont construits avec moyennes pour les épreuves d'environ 5 litres prises à toutes les profondeurs étudiées au jour marqué. \updownarrow indique que la valeur doit être augmentée, baissée. Les deux fractions de la population sont indiquées par les lignes — — — et ——— pour 1950. \times 1946, \otimes 1947, \square 1948, \circ 1950, \odot 1951.

Annual cycle for Cyclops, L. Ottsjön The abundance curves. Graph. 15 and 16, are constructed with averages for about 5 litres, calculated with all the samples from all depths sampled the day indicated. \updownarrow shows that the value ought to be increased, decreased. The two fractions of the Cyclops population are indicated by the lines — — — and ——— for the year 1950.



Graphique 15.



Graphique 16. Cycle annuel pour *Diaptomus* dans Ottsjön.

× 1946, ⊗ 1947, □ 1948, ○ 1950, ⊙ 1951.

Annual cycle for *Diaptomus*, L. Ottsjön.

Tableau 1. La transparence est évaluée au moyen d'un disque de SECCHI de 20 centimètres.

Lacs	Stations	Dates	Heures	Temps	Transparence
Sällsjön	A	30.5.46	18 h 30	Demi-couvert, pas soleil, vent faible	4.40
	A	31.5.46	13 h 30	Couvert, vent faible	4.60
	A	22.6.46	11 h	Couvert, calme	5.50
		27.6.46	8 h 30	Couvert, vent faible	5.50
	A	29.6.46	11 h	Couvert, calme, une petite pluie très fine	6.00
	B	29.6.46	15.45	Comme 11 h mais un vent faible	5.25
	A	25.7.45	15 h 30	Couvert, vent faible	7.10
Häckren	A	21.8.46	11 h	Sans nuages, vent faible	8.50
	A	2.7.46	12 h 40	Couvert, vent faible	6.20
	A	2.8.45	15 h	Couvert, calme	7.50
Gesten	A	17.8.51	10 h 45	Sans nuages, calme	7.00
	A	2.6.46	9 h 15	Couvert, vent faible une petite pluie	6.00
	A	1.7.46	13.45	Couvert, soleil voilé, vent	5.00—5.50
	A	1.7.46	17 h	Demi-couvert, soleil, vent faible	5.50
	A	1.8.51	10 h 30	Couvert, vent faible	4.80
	A	3.8.45	11 h 30	» » »	8.50
	A	16.8.51	17 h	Sans nuages calme	6.20
	A	23.8.46	12 h 30	Sans nuages, calme, soleil voilé	8.00
	A	7.10.46	12 h 15	Sans nuages, calme	8.50
Hotjön	A	2.6.46	15 h 45	Couvert, vent faible	5.00
	A	3.7.46	13 h 00	» » »	6.50
	A	3.7.46	19 h 30	Couvert, calme, une petite pluie	7.00
	A	5.7.46	11 h 45	Couvert, soleil voilé, vent	6.00
		6.7.46	9 h 30	Sans nuages, soleil voilé, vent faible	6.80
				Comme au dessus mais soleil clair	7.50
	A	4.8.45	15 h 30	Demi-couvert, soleil voilé, vent faible	8.20
	A	22.8.46	13 h 45	Sans nuages, vent	7.00
	A	6.10.46	14 h 30	Couvert, vent faible	7.25
	Ottsjön	A	27.5.50	12 h 30	Sans nuages, soleil voilé, vent faible
A		15.6.50	12 h	Couvert, vent faible	6.50
A		5.6.46	10 h	Demi-couvert, ensoleillé, vent fort	5.50
				Comme au dessus mais sans soleil	5.30
A		5.6.46	11 h 30	Demi-couvert, ensoleillé, vent fort	6.90
				Comme au dessus mais sans soleil	6.25—6.50
		15.6.46	12 h	Couvert, calme	6.50
		17.6.46	10 h	Sans nuages, calme	10.00
A		5.7.50	12 h	Demi-couvert, vent faible	7.00
		9.7.46	12 h 45	Presque sans nuages, vent	8.00
A		13.7.50	14 h	Demi-couvert, vent faible	7.50
A		28.7.51	12 h 30	Couvert, vent faible, pluie forte	5.25
				Comme au dessus mais sans pluie	6.20
		11.8.45	8 h	Sans nuages, soleil voilé, calme	9.10
Änn		A	15.8.51	15 h 30	Couvert, vent faible
	A	17.8.46	14 h 15	Couvert, calme	8.00
	A	21.8.50	17 h 30	Demi-couvert, sans soleil, vent faible	6.25
	A	3.10.46	13 h	Sans nuages, vent faible	7.50
	D	27.5.46	15 h 45	Sans nuages, calme	3.65
	G	6.6.46	18 h 30	Couvert, vent fort	0.50—0.75
	G	7.6.46	10 h	Couvert, vent faible	1.90
	A	11.6.46	10 h	» » »	4.50
	D	13.6.46	10 h	Couvert, vent	4.10
	A	13.7.46	13 h 30	Sans nuages, calme	8.10
	F	12.8.46	—	—	1.00
	D	13.8.46	20 h	Couvert, calme	7.00
	D-E	14.8.46	8 h 30	Couvert, vent faible	7.50
A	16.8.46	11 h 30	» » »	5.50	
A	1.10.46	10 h 30	Demi-couvert, soleilvoilé, vent	6.90	

Tableau 2. Le vent. On peut voir que les estimations diffèrent. La force du vent est sans doute aussi dépendante de conditions topographiques.

	Vent (échelle de Beaufort) selon le bureau météorologique de la Suède			Vent estimation par l'auteur		Vent (échelle de Beaufort) selon le bureau météorologique de la Suède			Vent estimation par l'auteur		
	Heure	Bil-hammaren	Storlien	Heure	Les endroits où sont prises les épreuves de plancton	Heure	Bil-hammaren	Storlien	Heure	Les endroits où sont prises les épreuves de plancton	
1946						10.6	10	3	3	12 —13	Fort
31.5	14	7	2	14 —15	Faible	10.6	13	5	3		
2.6				10 —10.30	»	15.6	13	4	4	15 —16	Faible
2.6	14	5	2	15 —16	»	16.6	19	3	0	19 —20	Calme
5.6	11	6	4	10.30—11.30	»	18.6	10	3	0	11 —17	Faible
6.6	17	6	0	16.30—17.30	Fort	18.6	13	5	3		
12.7	11	3	3	10	Faible	20.6	10	3	0	11 —13	Calme
13.7	14	3	0	13.30	Calme	4.7	10	5	3	9 — 9.30	(Fort-) Faible
16.8	11	2	3	11 —11.30	Faible	4.7	13	4	3	13 —13.30	Faible
17.8	14	1	2	14 —15	»	4.7	16	4	3	17.30—18	»
21.8	11	1	2	11 —12.30	»	5.7	01	3		01	»
22.8	14	3	3	14 —15	»	5.7	13	3	3	13.30	Calme
23.8	11	3	0	10 —14	Calme	15.7	13	6	4	12 —14	Fort
23.8	14	1	2			23.7	10	3	0	10.30—12	Calme
1.10	11	4	3	10.30—11	Faible	28.7	13	5	4	13 —14	Faible
3.10	14	4	3	13.30—14	»	14.8	10	4	3	10.30—12	»
6.10	14	1	4	14.30—15.30	»	15.8	10	5	0	11 —13	»
7.10	14	1	0	12 —13	Calme	17.8	10	7	4	11 —13	Fort
						21.8	10	3	0	10 —18	Faible-Calme
1947						21.8	13	3	0		
14.5	13	2	0		Faible	21.8	16	3	0		
21.7	16	1	3	16.45—19	»	22.8	10	2	0	12 —20	Faible-Calme
1948						22.8	16	4	3		
7.5	10	3	2	12 —13.30	Faible	23.8	13	4	0	13 —16	Faible
8.5	10	3	2	10 —14	Calme	25.8	13	9	5	13 —14	Fort
8.5	13	3	2			26.8	13	2	0	12.45—17.15	Calme
9.5	13	4	0	13 —15	Faible-Calme	26.8	16	2	0		
10.5	10	4	0	10.30—16	Faible	28.8	10	6	4	11.30—13	(Fort-) Faible
23.8	16	0	2	16 —19.30	Calme	30.8	01	1		0.30—02.00	Calme
23.8	19	1	0			1951					
24.8	13	3	2	12 —15	Faible-Calme	30.7	13	7	3	12 —15	Faible
25.8	10	2	2	11.30—17	»	31.7	13	3	0	12 —15	»
25.8	13	1	3			2.8	10	7	0	10 —11	Faible-Calme
25.8	16	1	2			4.8	16	5	0	16 —18	Faible
26.8	01	1		01 —02.30	Calme	5.8	13	6	4		»
26.8	13	2	0	13.45—16	Faible-Calme	11.8	13	6	3	12 —14	Fort
25.10	13	8	3	12 —15	Faible-Fort	15.8	01	2		0.30—01.30	Faible-Calme
26.10	01	1		01	Calme	15.8	13	3	2	15.30—16	Faible
1950						16.8	16	3	2	17.30—18.30	Faible-Calme
10.5	13	3	4	13 —15	Faible	17.8	10	2	0	10.45—14	Faible
12.5	10	4	3	10 —12	Fort	17.8	13	3	2		
26.5	16	5	4	16 —17	»	20.8	10	8	3	11.30—14.30	Fort
27.5	10	2	3	12 —13	Faible-Calme	20.8	13	9	4		

Tableau 3. Teneur en oxygène. Exprimée en mg/litre.

Lac	Sällsjön				Gesten			
	A	A	C	A	A	F	B	A
Station	31.5.46	21.8.46	21.8.46	18.2.47	2.6.46	23.8.46	23.8.46	23.8.46
Date	17	17	1 1/2	17	25	1 1/2	25	21
Profondeur total en mètres								
Surface	11.4	9.4	9.7	15.2	11.1	9.5	10.1	9.5
5 m.	11.2	9.5	—	—	11.0	—	—	9.5
10 »	—	9.2	—	—	—	—	—	9.5
15 »	11.7	9.0	—	—	—	—	—	9.4
20 »					11.2		9.4	9.3

Lac	Hottön				Ånn	
	A	A	A	A	A	A
Station	2.6.46	22.8.46	6.10.46	18.6.50	16.8.46	1.10.46
Date	46	45	47	45	17	17
Profondeur totale en mètres						
Surface	10.2	9.6	—	11.1	9.7	10.9
5 m.	9.3	9.7	—	—	9.6	10.7
10 »	10.6	9.7	—	—	9.7	10.9
15 »	11.2	9.7	—	11.2	9.7	10.9
20 »	11.4	9.8	—	—		
25 »	—	—	—	11.1		
30 »	11.4	10.6	10.1	—		
35 »	—	—	10.2	—		
40 »	11.5	—	—	—		
45 »			10.0			
0.2—1 m. au dessus du fond	—	10.5	—	11.3		

Lac	Ottsjön										
	A	A	H	A	A	A	A	A	X	T	A
Station	5.6	17.8	17.8	3.10	28.5	11.6	15.6	13.7	21.8	21.8	28.8
Date	1946	1946	1946	1946	1950	1950	1950	1950	1950	1950	1950
Profondeur totale en mètres.....	26	27	1—2	29	29	29	29	27	1/2	1/2	29
Surface	11.2	9.5	9.7	10.6	11.8	11.3	—	10.3	9.4	10.4	9.7
5 m.	11.3	9.5		10.7	11.7	11.2	11.2	10.3			9.7
10 »	11.4	9.4		10.8	11.9	11.2	—	10.3			9.7
15 »	11.8	9.5		11.4	—	11.3	—	10.3			9.7
20 »	12.0	9.4		10.6	11.8	11.3	—	10.3			9.7
25 »	—	9.3		10.7	—	—	—	—			—
0.2—1 m. au dessus du fond	—	—		—	11.8	11.3	11.2	10.2			9.7

Tableau 4. La conductibilité.

Laes	Stations	Dates	Conductibilité $\times 18$	La couche	Prof. tot.
Kallsjön	A	27.3.46	19.9×10^{-6}	40 m	52
Gevsjön.....	A	14.5.47	26.7×10^{-6}	Surface-3 m	1-3
		14.5.47	27.0×10^{-6}	» -3 »	1-3
		14.5.47	26.2×10^{-6}	» -3 »	1-3
Ånn	A	31.3.46	37.9×10^{-6}	Près de la surface	18
		31.3.46	38.2×10^{-6}	Près du fond	18
		F 2.10.46	39.5×10^{-6}	Près de la surface	1
Sällsjön.....	A	18.2.47	24.1×10^{-6}	Près du fond	17
		28.3.46	25.4×10^{-6}	5 m prof.	11
Gesten	A	29.3.46	26.0×10^{-6}	Près du fond	20
		23.8.46	18.3×10^{-6}	» de la surface	21
		7.10.46	19.8×10^{-6}	» » » »	25
Hottön	A	18.6.50	16.1×10^{-6}	Près de la surface	45
			22.6×10^{-6}	Près du fond	45
		23.8.50	17.9×10^{-6}	Près de la surface	46
			21.2×10^{-6}	Près du fond	46
		6.10.46	19.8×10^{-6}	Près de la surface	47
Ottsjön	A	16.2.47	21.0×10^{-6}	14 m prof.	25
		30.3.46	25.3×10^{-6}	??	25
		28.5.50	22.2×10^{-6}	Près de la surface	29
			22.2×10^{-6}	» » » »	29
			21.7×10^{-6}	Près du fond	29
Ottsjön	A	20.6.50	19.8×10^{-6}	Près de la surface	29
			20.7×10^{-6}	Près du fond	29
		5.7.50	18.9×10^{-6}	Près de la surface	29
			19.3×10^{-6}	Près du fond	29
		31.7.50	19.0×10^{-6}	Près de la surface	29
			17.8×10^{-6}	Près du fond	29
		30.8.50	18.8×10^{-6}	Près de la surface	29
			18.7×10^{-6}	Près du fond	29
		3.10.46	18.7×10^{-6}	Près de la surface	29

Tableau 5. Le pH. He indique que le pH est évalué au moyen d'un comparateur à disques de verre coloré de HELLIGE. Ta indique que cela est fait avec un TAYLOR *water analyzer*. Dans les deux cas le bleu de bromothymol est employé.

Lacs	Stations	Dates	pH près de la surface	pH près du fond	Profondeur totale	Méthode
Sällsjön	A	18.2.47	6.4	6.5	17	He
	A	1.6.46	6.8	6.8	17	He
	A	21.8.46	6.6	6.5	17	He
Gesten	A	2.6.46	6.7	6.7	25	He
	B	23.8.46	6.5	6.5	25	He
	A	23.8.46	6.5	6.5	21	He
	A	7.10.46	6.7	6.7	25	He
Hottön	A	2.6.46	6.7	6.7	46	He
	A	18.6.50	6.6	6.6—6.7	45	Ta
	A	22.8.46	6.7	6.3	45	He
	A	6.10.46	6.5	6.3	47	He
Ottsjön	A	16.2.47	6.4	6.4 (Prof. 14 m.)	25	He
	A	5.6.46	6.8	6.7	26	He
	A	10.6.50	7.0	—	29	Ta
	A	13.7.50	7.0	7.2	27	Ta
	A	14.8.50	7.1	6.8	29	Ta
	R	15.8.50	7.1	—	1/2	Ta
	A	17.8.46	6.8	6.7	29	He
	X	21.8.50	7.5	—	1/2	Ta
	T	21.8.50	7.2	—	1/2	Ta
	G	21.8.50	7.2	—	1/2	Ta
	A	22.8.50	7.0	—	29	Ta
A	3.10.46	6.7	6.7	29	He	
Ånn	A	6.6.46	6.8	6.8	17	He
	D	13.8.46	6.8	6.8	20	He
	A	16.8.46	6.8	6.8	17	He
	A	1.10.46	6.6	6.6	17	He

Tableau 6. L'alcalinité. Le dosage est fait en titrant les échantillons (100 cm³) par HCl en présence de méthylorange.

Lacs	Stations	Dates	Cm ³ 0.1-n HCl/litre d'eau		Profondeur totale
			près de la surface	près du fond	
Sällsjön	A	31.5.46	3.1	4.0	17
	A	1.6.46	—	2.0	17
	A	21.8.46	1.6	1.7	17
Gesten	A	2.6.46	2.4	1.7	17
	A	23.8.46	1.8	1.8	21
	A	7.10.46	1.9	2.0	25
Hottön	A	2.6.46	2.1	2.4	46
	A	22.8.46	1.9	1.9	45
	A	18.6.50	—	2.4	45
	A	6.10.46	2.9, 2.6	1.9	47
Ottsjön	A	5.6.46	1.7	1.8	26
	A	27.5.50	3 ou 4	3 3 4?	26
	A	28.5.50	3	—	29
	A	10.6.50	2.5, 2.7	—	29
	A	15.6.50	2.3	2.2, 2.3	29
	A	16.6.50	{2.5, 3.6, 2.4, 2.7, } {2.8, 2.5, 2.5}	—	29
	A	13.7.50	2.6, 2.8	2.7	27
	A	14.8.50	2.6	2.5	29
	R	15.8.50	2.8	—	1/2
	A	17.8.46	2.0	1.8	29
X	21.8.50	6.5—7.5	—	1/2	
T	21.8.50	2.9	—	1/2	
A	22.8.50	2.8	—	29	
A	3.10.46	2.1	2.1	29	
Ånn	A	6.6.46	1.7	1.7	17
	A	16.8.46	2.3	1.6	17
	A	1.10.46	2.2	—	17

Le moment précis du virage du méthylorange est un peu difficile à noter. Il est possible que certaines des évaluations de la valeur d'alcalinité calculées en 1946 doivent être augmentées d'environ 1/2 cc.

Table 7. La durété totale. Le dosage des sels alcalino-terreux en bloc est fait avec la solution de Savon de Clarke.

Lacs	Stations	Dates	cm ³ solution de savon pour 100 cm ³	Degrés allemand	Profondeur de l'épreuve	Prof. tot.
Sällsjön	A	21.8.46	3	0.40	Près de la surface	17
			3—4	0.40—0.65	Près du fond	17
Gesten	A	23.8.46	4	0.65	Près de la surface	21
			3	0.40	Près du fond	21
	A	7.10.46	3—4	0.40—0.65	Près de la surface	25
			3—4	0.40—0.65	Près du fond	25
Hottön ...	A	22.8.46	3	0.40	Près de la surface	45
			3	0.40	Près du fond	45
	A	6.10.46	4	0.65	Près de la surface	47
			4	0.65	Près du fond	47
Ottsjön ...	A	17.8.46	3	0.40	Près de la surface	29
			3	0.40	Près du fond	29
	A	3.10.46	4	0.65	Près de la surface	29
			4	0.65	Près du fond	29
Ånn	A	16.8.46	3	0.40	Près de la surface	17
			3—4	0.40—0.65	Près du fond	17
	A	1.10.46	5	0.90	Près de la surface	17
			4	0.65	Près du fond	17

Tableau 8. Matières organiques. Le pouvoir réducteur vis à vis du permanganate est évalué comme une estimation de l'abondance en matière organiques. L'eau à étudier n'est pas filtrée. La réduction est faite avec une solution de permanganate de potassium à ébullition en milieu acide. En multipliant N par 8 on obtient la teneur en oxygène consommé, exprimée en gramme par litre.

Lacs	Stations	Dates	N		Profondeur totale
			près de la surface	près du fond	
Sällsjön	A	21.8.46	0.0016	0.0011	17
Gesten	A	7.10.46	0.0011	0.0009	25
Hottön	A	22.8.46	0.0010	0.0011	45
	A	6.10.46	0.0013	0.0008	47
	A	18.6.50	0.0001	0.0008	45
Ottsjön	A	27.5.50	0.0005	0.0007	26
	A	15.6.50	0.0010	0.0006	29
	A	13.7.50	0.0007	0.0006	27
	A	17.8.46	0.0011	0.0018	27
	X	21.8.50	0.0017	—	1/2
	T	21.8.50	0.0003	—	1/2
	A	21.8.50	0.0005	0.0005	29
Ånn	A	3.10.46	0.0008	0.0008	29
	A	16.8.46	0.0011	0.0011	17
	A	1.10.46	0.0006	0.0009	17

Häckren

31.7.51. 5.8.51.

Lac	Date	31.7.51.										5.8.51.												
		E 1-2 m	15 h	B 2 m	13 h	C 2 m	14 h	A	17 m	16 h	16 h	0	0	0	2	2	2	5	5	10	10	10	16	16
Stat. Heure, Prof. tot.		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prof. de l'épreuve																								
Diapt. lat. ad. ♂♂							1																	
Di. copépodites																								1
Centrop. nauplii									1															
Cyclopidae naupl.										1														6
Cy. copépodites jeun.											1													4
Cy. copépodites âgés																								1
Cyclops scut. ad. ♂♂																								6
Cy. s. ad. ♀♀ avec																								2
Da. l. h. ad. ♀♀ avec																								1
Da. l. h. ad. ♀♀ sans																								1
Da. l. h. ♀♀ jeun. & ♂♂			2	1		1				2	1	4	6											3
♂♂ séparabl. du g. p.																								
Bosmina coregoni			1	2	1		1	1	1	1	1	1	1	1	1	4	3	26	env.	34	8	38	30	11
♀♀ avec . . . (incl. . . .)																		390	5	28	1	4	1	2

Häckren

17.8.51.

Lac	Date	17.8.51.																						
		A 17 m	11-12 h	30	B 2 m	13 h	D 3-5 m	14 h	C 4 m	14 h	0	3												
Stat. Heure, Prof. tot.		0	0	0	2	2	5	5	10	10	10	16	16	16	1	1	1	1	1	1	1	1	1	
Prof. de l'épreuve																								
Di. copépodites																								
Cyclopidae naupl.																								
Cy. copépodites jeun.																								
Cy. copépodites âgés																								
Cyclops scut. ad. ♂♂																								
Cy. s. ad. ♀♀ avec																								
Da. l. h. ad. ♀♀ avec																								
Da. l. h. ad. ♀♀ sans																								
Da. l. h. ♀♀ jeun. & ♂♂																								
♂♂ séparabl. du g. p.																								
Bosmina coregoni																								
♀♀ avec . . . (incl. . . .)																								

Le volume pour chacune des épreuves ci-dessus est de 5 litres 3.

Lac	Hottön																													
	2.6.46.				22.8.46.				6.10.46.				21.7.47.																	
	A 46m		15h-16h		A 45m		14h-15h		A 47m		14h 30-15h 30		A-B 38m		16h 30-17h 30															
Stat. Heure. Prof. tot.	0	5	10	15	20	30	40	0	5	10	15	20	25	35	44	0	5	10	15	20	25	35								
Prof. de l'épreuve	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10								
Volume																														
Diapt. lat. ad.																														
Di. copépodites																														
Centrop. nauplii																														
Nauplii	1	69	31	9	2																									
Cyclopidae naupl.																														
Cy. copépodites jeun.	1	35	1	2																										
Cy. non classifiés																														
Cyclops scut. ad. ♂♂																														
Cv. s. ad. ♀♀ sans	1	2																												
Cv. s. ad. ♀♀ avec	1																													
Daph. long. hyal.																														
Da. l. h. sans	2	14	49	53	11	33																								
Da. l. h. ad. ♀♀ avec	1	2																												
Bosmina coregoni	5	2	13	71	28	3																								
♀ avec ... (incl.)	1	1	1	1																										

Lac	Hottön																																
	21.7.47.				10.5.48.																												
	A 50m		18h 30		A 50m		10h 30-13h 30																										
Stat. Heure. Prof. tot.	0	5	10	0	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5											
Prof. de l'épreuve	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10											
Volume																																	
Di. l. ad. ♂♂	1																																
Di. copépodites	1																																
Centrop. nauplii	2	1	2	1	2	1	2	2	1																								
Cyclopidae naupl.																																	
Cy. copépodites jeun.	2	1	6	5	3	4	8	2	5	4	4	6	2	7	3	2	1	2	4	3	1	10	4	3	2	8	5						
Cy. copépodites âgés	18	9	9																														
Cy. non classifiés																																	
Cyclops scut. ad. ♂♂																																	
Cv. s. ad. ♀♀ sans	1																																
Da. l. h. sans	18	3	1																														
Da. l. h. ad. ♀♀ avec	65	3																															
Da. l. h. ♀♀ jeun. & ♂♂																																	
♂♂ séparabl. du g. P. ...																																	
Bosmina coregoni	3	7	2	1	2	4	2	1																									
♀ avec ... (incl.)	2																																

Lac	Hottön																
	9.3.50.						8.5.50.										
	C 40m 11h		B 40m 14h		A 47m 13h		D 7-10m 13h		B 27m 15h-17h								
Stat. Heure. Prof. tot.	Prof. de l'épreuve	1	5	10	15	20	25	35	45	1	5	10	15	20	26		
Centrop. nauplii																	
Cyclopidae naupl.		12	42	73	41	80	3	4	51	1	1	4	28	13	40	37	55
Cy. copépodites jeun. ...		1									1						
Cy. copépodites âgés				5		1											
Bosmina coregoni																	
♀ avec ... (incl. ...)																	

Le volume pour chacune des épreuves ci-dessus est de 5 litres 3.

Lac	Hottön																		
	8.5.50						18.6.50						23.8.50						
	B 27m 15h-17h		A 45m 15h-17h		D 10m 13h 30		A 47m 13h		D 10m 13h 30		A 47m 13h		A 47m 13h		A 47m 13h		A 47m 13h		
Stat. Heure. Prof. tot.	Prof. de l'épreuve	1	5	10	15	20	25	35	44	5	44	0	5	10	15	20	25	35	45
Di. l. ad. ♀ sans																			
Di. copépodites																			
Centrop. nauplii																			
Cyclopidae naupl.		2		3	1														
Cy. copépodites jeun. ...																			
Cy. copépodites âgés																			
Cyclops scut. ad. ♂♂																			
Cy. s. ad. ♀ sans																			
Cy. s. ad. ♀ avec																			
Da. l. h. ad. ♀ avec																			
Da. l. h. ad. ♀ sans																			
Da. l. h. ♀ jeun. & ♂♂																			
♂♂ séparabl. du g. P. ...																			
Bosmina coregoni																			
♀ avec ... (incl. ...)																			

Le volume pour chacune des épreuves ci-dessus est de 5 litres 3 sauf pour l'épreuve du 18.6.50, 5 m. à droite, qui est de 1 litre 6.

Lac	Hottön												Ottsjön								
	23.8.50						5.6.46						12.7.46								
	B 28m 14h		C 36m 15h		A-B 14h		B-C 15h		A 26m 11h		A 28m 10h		5.6.46		12.7.46						
Stat. Heure. Prof. tot. Prof. de l'épreuve	0	2	5	10	15	20	25	35	0	2	5	10	15	20	25	0	5	10	15	20	25
Di. l. ad. ♂♂	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Di. l. ad. ♀♀ sans	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Di. copépodites	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Centrop. nauplii	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nauplii	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cyclopidæ naupl.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cy. copépodites jeun.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cy. copépodites âgés	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cy. non classifiés	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cyclops scut. ad. ♂♂	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cy. s. ad. ♀♀ sans	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cy. s. ad. ♀♀ avec	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Da. l. h. sans	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Da. l. h. ad. ♀♀ avec	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Da. l. h. ad. ♀♀ sans	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Da. l. h. ♀♀ jeun. & ♂♂	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♂♂ séparabl. du g. p.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bosmina coregoni	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♀♀ avec . . . (incl. . . .)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Le volume pour chacune des épreuves ci-dessus est de 5 litres 3 (Hottön) ou de 10 litres (Ottsjön).

Ottstjön
4.7.50

Lac	Date	A 27m 9h		A 27m 13h					E 21m 14h					S 3m 15h					U 1m 15h					V 8m 15h					X 1m 16h				
		0	2	5	10	15	20	25	0	2	5	10	15	20	25	0	5	10	15	20	0	3	0	3	0	3	0	3	0	7	0	0	0
Di. l. ad. ♂ sans														1																			
Di. l. ad. ♀ sans			1	1						2				2																			
Cyclopidae naupl.		23	31	24	28	34	31	28	10	20	12	26	17	17	20	19	71	18	17	22	1				1						1		1
Cy. copépodites jeun.		3	1									1		1	2					2													
Cy. copépodites âgés		15	21	10	18	13	15	9	3	23	15	21	15	17	4	3	2	31	28	4	1				1								
Cyclops scut. ad. ♂♂				1		1	2					1		3	2			1	1	2													
Cy. s. ad. ♀ sans			1	1	1	1								1	1	1																	
Cy. s. ad. ♀ avec		1	1	1	1	1				2	1	1	1	1				1		1													
Da. l. h. ad. ♀ avec		1	1	1	1					1	1	1	1	1																			
Da. l. h. ad. ♀ sans					2	4	3				5	3	1	1				2	4														
Da. l. h. ♀ jeun. & ♂♂		1	5	8	6	3	8	7			5	4	5	5	5	1	3	3	4	2													
♂♂ séparabl. du g. p. ...																																	
Bosmina coregoni ...		2	15		2	8	5	8			23	5	2	5	1	7	22	6	17	37					4								
♀ avec ... (incl. . . .)																													12	3	3		

Le volume pour chacune des épreuves ci-dessus et ci-dessous est de 5 litres 3.

Ottstjön
4.7.50

Lac	Date	A 27m 18h					A 27m 22h					A 27m 1h					M 23m 13h					G 1m 12h												
		0	2	5	10	15	20	25	0	2	5	10	15	20	25	0	2	5	10	15	20	25	0	5	10	15	22	0	1	1	2	0	0	
Di. l. ad. ♂♂							1							1							1		1	2							2			
Di. l. ad. ♀ sans																							1											
Di. copépodites											1													1										
Cyclopidae naupl.		21	20	19	37	22	13	11	21	20	28	14	21	11	42	15	9	29	32	18	38	15	13	46	23	22	49	2	4					
Cy. copépodites jeun.							1			1	1			1			2								1	1								
Cy. copépodites âgés		4	23	16	12	11	15	18	1	7	10	12	8	5	6	4	16	9	18	10	21	21	3	15	8	5	8							
Cyclops scut. ad. ♂♂		1	1	1	1			2										1	2	2	1				2	1								
Cy. s. ad. ♀ sans		1	1	1	2	1					1	1	1	2	1	1	1	1	3	1														
Cy. s. ad. ♀ avec				1	1	2	1					1	1	2	1	1	1	1	1	1								2	6	6	2			
Da. l. h. ad. ♀ avec		1	4	1	1	1	4			1		2	2	1				2	3	4	1	1												
Da. l. h. ad. ♀ sans		2	1	2	2	5	9			6				2		1	4	1	3	4	2	1						1	1					
Da. l. h. ♀ jeun. & ♂♂		1	7	2	4		7	3		7	1	1	1	2		1	7	7	4	3	6	3	1	6	2	7	5							
♂♂ séparabl. du g. p. ...																																		
Bosmina coregoni		2	10	8	2	4	13	2	2	15	9	9	8	5	1	8	6	5	11	2	8	2				1	1	7	17		4	3		
♀ avec ... (incl. . . .)																																		

Lac	Ottsjön													
	15.8.50							17.8.50						
	M 21m 11h 0 5 10 15 20	N 17m 13h 0 5 10 15	O 10-5m 13h 0 5 8 0 4	P, Q 1m 13h 0 0 0 0	R 1/2m 15h 0	A 30m 11h-12h 0 0 0 2 2 5 5 10 10 15 15 20	*	*	*	*	*	*	*	*
Date														
Stat. Heure. Prof. tot. Prof. de l'épreuve														
Di. l. ad. ♂♂ sans	2	1	1	1	1	1	1	1	1	1	1	1	1	1
Di. l. ad. ♀♀ sans	3	3	1	2	1	1	1	1	1	1	1	1	1	1
Cyclopidæ naupl.	6 32 14 25 38	14 39 23 15	18 20 4 26 38	11 20 11 8	—	25 24 31 14 25 16 37 29 40 32 51 53	—	—	—	—	—	—	—	—
Cy. copépodites âgés	—	2	1	1	1	—	—	—	—	—	—	—	—	—
Cyclops scut. ad. ♂♂	1 2 1 3	2 1 1 1	3 3 2	— 1 1 1	—	1 2 2 3 2 4 3 2 5 4 3 5	—	—	—	—	—	—	—	—
Cy. s. ad. ♀♀ sans	1	2	6	1	1	—	—	—	—	—	—	—	—	—
Cy. s. ad. ♀♀ avec	—	4 5	3	2	1	—	—	—	—	—	—	—	—	—
Da. l. h. ad. ♀♀ avec	—	2	2	1	3	—	—	—	—	—	—	—	—	—
Da. l. h. ad. ♀♀ sans	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Da. l. h. ♀♀ jeun. & ♂♂	3	3	10	1	2	—	—	—	—	—	—	—	—	—
♂♂ séparabl. du g. p. ...	—	2	6	1	1	—	—	—	—	—	—	—	—	—
Bosmina coregoni	2	—	1	—	2	—	—	—	—	—	—	—	—	—
♀♀ avec . . . (incl. . . .)	1	—	—	—	—	—	—	—	—	—	—	—	—	—

Le volume pour chacune des épreuves ci-dessus et ci-dessous est de 5 litres 3.

Lac	Ottsjön													
	17.8.50							21.8.50						
	A 30m 11h-12h 20 25 29 29	L 3m 13h 0 0 0 0	F 2m 13h 0 0 0	E 17m 14h 0 0 5 5 10 10 15 15	X 0.3-1m 10h 0 0 0 0 0 0	Y 2-3m 11h 0 2 0 0 0	*	*	*	*	*	*	*	*
Date														
Stat. Heure. Prof. tot. Prof. de l'épreuve														
Di. l. ad. ♂♂ sans	3	—	—	—	—	—	—	—	—	—	—	—	—	—
Di. l. ad. ♀♀ sans	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Cyclopidæ naupl.	62 13 28 14	14 12 29	1 4	10 17 33 38 37 27 53 73	2 4 2 1	—	—	—	—	—	—	—	—	—
Cy. copépodites jeun. ...	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Cy. copépodites âgés	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cyclops scut. ad. ♂♂	5	1	—	—	—	—	—	—	—	—	—	—	—	—
Cy. s. ad. ♀♀ sans	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cy. s. ad. ♀♀ avec	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Da. l. h. ad. ♀♀ avec	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Da. l. h. ad. ♀♀ sans	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Da. l. h. ♀♀ jeun. & ♂♂	—	6	—	—	—	—	—	—	—	—	—	—	—	—
♂♂ séparabl. du g. p. ...	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Bosmina coregoni	2 8 3 1	—	—	—	—	—	—	—	—	—	—	—	—	—
♀♀ avec . . . (incl. . . .)	—	1	—	—	—	—	—	—	—	—	—	—	—	—

env. 14 3 1 73
1.300
2 env. 50

Lac	Ottsjön													
	21.8.50						22.8.50							
Date	Ä 1-3 m 12h	Ä 1 m 12h	Z 5 m 13h	A-B-C-D 26-29m	17h	G 0.5-1 m 18h						A-B-C-D 26-29m	12h 30	
Stat. Heure. Prof. tot. Prof. de l'épreuve	0 0 0 0 0	0 0 0 0 0	0 4 0 4 0 4	0 0 0 0 0 4	0 0 0 0 0 0	0 0 0 0 0	0 0 0 0 0						0 0 0 0 0	2 2 5
Di. l. ad. ♂♂	—	—	—	—	—	8 6 5	5 8						1 2	— 2 1
Di. l. ad. ♀♀ sans	—	—	—	—	—	10 12 4	2 13 10						3 2	— 2 1
Di. l. ad. ♀♀ avec	1	—	—	—	—	1 3	1						1	—
Di. copépodites	—	—	—	—	—	—	—						—	—
Cyclopidae naupl.	25 46 13 60 35	1 3 10 7	1 24 1 26 3 31	—	—	—	1						—	— 28 4
Cy. copépodites jeun.	1 4 4 3 1	—	—	—	—	—	—						—	—
Cyclops scut. ad. ♂♂	2	—	—	—	—	—	—						—	— 7 7
Cy. s. ad. ♀♀ sans	1	—	—	—	—	—	—						—	— 7 4 1
Cy. s. ad. ♀♀ avec	—	—	—	—	—	—	—						—	— 2 2 2
Da. l. h. ad. ♀♀ avec	—	—	—	—	—	—	—						—	— 14 4
Da. l. h. ad. ♀♀ sans	—	—	—	—	—	—	—						—	— 10 3
Da. l. h. ♀♀ jeun. & ♂♂	—	—	—	—	—	—	—						—	— 1 1
♂♂ séparabl. du g. p.	—	—	—	—	—	—	—						—	—
Bosmina coregoni	1 1 10 4	—	—	—	—	—	—						—	— 1 3
♀♀ avec ... (incl. . . .)	—	—	—	—	—	—	—						—	—

Le volume pour chacune des épreuves ci-dessus et ci-dessous est de 5 litres 3.

Lac	Ottsjön													
	22.8.50						25.8.50							
Date	A 27m 17h 30	C 26m 18h	D 29m 19h	C-D 19h						A 30m 13h-14h	7 10 15			
Stat. Heure. Prof. tot. Prof. de l'épreuve	0 2 5 10 15 20 26	0 2 5 10 15 20 25	0 2 5 10 15 20 28	0						0 0 0 1 2 3.5 5	7 10 15			
Di. l. ad. ♂♂	1	—	—	—	—	—	—						—	—
Di. l. ad. ♀♀ sans	2 3 2	—	—	—	—	—	—						—	— 1
Di. l. ad. ♀♀ avec	—	—	—	—	—	—	—						—	— 1
Cyclopidae naupl.	1 14 39 27 34 28 36	15 23 109 49 60 43 ?	19 13 42 47 37 98	26						11 29 34 30 36 16 36 32 40 48	—			
Cy. copépodites jeun.	—	—	—	—						—	— 1 1 2 2 3 3 1 3 3			
Cy. copépodites âgés	—	—	—	—						—	— 1			
Cyclops scut. ad. ♂♂	—	—	—	—						—	— 1 2 6 — 1 3 2 1 2			
Cy. s. ad. ♀♀ sans	5 1 2 11 2 1	3 5 1 5 4 4	2 3 2 2	—						—	— 2 1 3 1 4 2 4 4 3			
Cy. s. ad. ♀♀ avec	6 2 11 6 1	—	—	—						—	— 2 1 — 2 1 1 1 1			
Da. l. h. ad. ♀♀ avec	1 3 9 3 1	—	—	—						—	— 2 1 — 2 1 1 1 1			
Da. l. h. ad. ♀♀ sans	1 10 3	—	—	—						—	— 3 — 1 1 — 1 1 2			
Da. l. h. ad. ♀♀ jeun. & ♂♂	4 1 1	—	—	—						—	— 4 1 1 — — 1 1 2			
♂♂ séparabl. du g. p.	1 2 1	—	—	—						—	— 1 3 2 4 2 1 2 1 1			
Bosmina coregoni	1 1 1	—	—	—						—	— 2 — 2 — 1 — 1			
♀♀ avec ... (incl. . . .)	—	—	—	—						—	— 1 — 1 — 1 — 1			

Lac	Kallsjön			Gevsjön			Ånn													
	27.3.46			14.5.47			* 31.3.46		* 6.6.46		* 13.7.46		* 16.8.46		* 10-18m 11h					
Date	A 52m 11h-14h			A 2-3m			A 18m 13h 30		A 17m 17h		A 16m 13h 30		G 2m F 1m		B 10-18m 11h					
Stat. Heure. Prof. tot.	10	20	30	40	50	0	2	0	1	0	0	1	5	10	15	0	0	0	0	0
Prof. de l'épreuve	20	20	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
Volume	1	6	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	
Diapt. lat. ad.	—	2	—	—	—	—	3	3	1	—	—	—	—	—	—	—	—	—	—	
Di. I. ad. ♂♂	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Di. copépodites	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Centrop. nauplii	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Nauplii	11	53	15	6	11	—	28	39	50	86	—	—	—	—	—	—	—	—	—	
Cyclopidae naupl.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Cy. copépodites jeun.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Cy. non classifiés	15	10	1	2	6	1	1	1	1	—	—	—	—	—	—	—	—	—	—	
Cyclops scut. ad. ♂♂	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Cy. s. ad. ♀♀ sans	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Cy. s. ad. ♀♀ avec	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Daph. long. hyal.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Da. I. h. sans	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Da. I. h. ad. ♀♀ avec	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Bosmina coregoni	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
♀♀ avec . . . (incl. . . .)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	

¹ Épreuve un peu incomplète.

Lac	Ann									
	16.8.46		1.10.46		7.5.48					
	A 18m 11h 30	A 17m 11h	E 2m 12h Bord de la glace	E 2m 12h Bord de la glace	E 2m 12h 30 Bord de la glace	E 2m 14h Bord de la glace	E 1--2m 15h Eau libre	*	*	*
Date	0 5 15	0 5 10 15	1 1 1 1 1	1 1 1 1 1	1 1 1 1 1	1 1 1 1 1	1 1 1 1 1	1 1 1 1 1	1 1 1 1 1	1 1 1 1 1
Stat. Heure. Prof. tot.	10 10 10	10 10 10 10	25 25 25 25 25	25 25 25 25 25	10 10 10 10 10	10 10 10 10 10	10 10 10 10 10	10 10 10 10 10	10 10 10 10 10	10 10 10 10 10
Prof. de l'épreuve	1 — 13		1 — — — —	1 — — — —	— — — — —	— — — — —	— — — — —	— — — — —	— — — — —	— — — — —
Volume										
Diapt. lat. ad.										1
Di. l. ad. ♂♂										
Di. l. ad. ♀♀ sans										
Di. l. ad. ♀♀ avec										
Di. copépodites	—	3	—	—	—	—	—	—	—	—
Centrop. nauplii	—	6	2	4	1	3	2	—	2	1
Nauplii	45	32	229							
Cyclopidae naupl.		38	15	17	11	5	6	3	2	7
Cy. copépodites jeun.						—	—	—	—	—
Cy. copépodites âgés						3	2	2	1	5
Cy. non classifiés						—	—	—	—	—
Cy. s. ad. ♀♀ sans						—	—	—	—	—
Cy. s. ad. ♀♀ avec						—	—	—	—	—
Daph. long. hyal.						—	—	—	—	—
Da. l. h. sans						—	—	—	—	—
Da. l. h. ad. ♀♀ avec						—	—	—	—	—
Da. l. h. ♀♀ jeun. & ♂♂						—	—	—	—	—
♂♂ séparabl. du g. p.						—	—	—	—	—
Bosmina coregoni	5	1	6	4	—	—	—	—	—	—
♀♀ avec . . . (incl. . . .)						—	—	—	—	—

Lac	Ann											
	8.5.48											
	D 13 m 10h—14h											
Date	Bord de la glace			Eau libre			Bord de la glace			Eau libre		
Stat. Heure. Prof. tot.	0	5	10	0	5	10	0	5	10	0	5	10
Prof. de l'éprouve	0	5	10	0	5	10	0	5	10	0	5	10
Volume	0	5	10	0	5	10	0	5	10	0	5	10
Di. l. ad. ♂	1	—	—	—	—	—	1	—	—	—	—	—
Di l. ad. ♀ sans	—	—	—	—	—	—	—	—	—	—	—	—
Di l. ad. ♀ avec	—	—	—	—	—	—	—	—	—	—	—	—
Di. copépodites	—	—	—	—	—	—	—	—	—	—	—	—
Centrop. nauplii	1	4	1	3	1	—	1	—	—	—	—	—
Cyclopidæ naupl.	4	1	7	6	1	—	5	8	3	4	2	3
Cy. copépodites jeun.	3	1	11	9	1	—	6	3	1	—	3	7
Cy. copépodites âgés	—	17	5	—	—	—	7	4	7	2	5	5
Da. l. h. ♀♀ jeun. & ♂♂	—	3	2	3	—	—	—	1	1	3	—	1
♂♂ séparabl. du g. p.	—	—	—	—	—	—	—	—	—	—	—	—
Bosmina coregoni	—	2	2	3	—	—	—	—	—	—	—	—
♀♀ avec . . . (incl. . . .)	—	—	—	—	—	—	—	—	—	—	—	—

Lac	Ann											
	23.8.48											
	C 25m 16h—19h 30											
Date	Bord de la glace			Eau libre			Bord de la glace			Eau libre		
Stat. Heure. Prof. tot.	0	5	10	0	5	10	0	5	10	0	5	10
Prof. de l'éprouve	0	5	10	0	5	10	0	5	10	0	5	10
Volume	0	5	10	0	5	10	0	5	10	0	5	10
Di. l. ad. ♂	2	—	—	—	—	—	1	—	—	—	—	—
Di l. ad. ♀ sans	—	5	1	—	—	—	—	—	—	—	—	—
Di l. ad. ♀ avec	—	—	—	—	—	—	—	—	—	—	—	—
Di. copépodites	—	—	—	—	—	—	—	—	—	—	—	—
Centrop. nauplii	—	—	—	—	—	—	—	—	—	—	—	—
Cyclopidæ naupl.	—	—	—	—	—	—	—	—	—	—	—	—
Cy. copépodites jeun.	1	—	—	—	—	—	—	—	—	—	—	—
Cy. copépodites âgés	1	—	—	—	—	—	—	—	—	—	—	—
Cy. s. ad. ♀♀ sans	—	—	—	—	—	—	—	—	—	—	—	—
Cy. s. ad. ♀♀ avec	—	—	—	—	—	—	—	—	—	—	—	—
Da. l. h. ad. ♀♀ avec	—	—	—	—	—	—	—	—	—	—	—	—
Da. l. h. ad. ♀♀ sans	—	—	—	—	—	—	—	—	—	—	—	—
Da. l. h. ♀♀ jeun. & ♂♂	—	—	—	—	—	—	—	—	—	—	—	—
♂♂ séparabl. du g. p.	—	—	—	—	—	—	—	—	—	—	—	—
Bosmina coregoni	—	—	—	—	—	—	—	—	—	—	—	—
♀♀ avec . . . (incl. . . .)	—	—	—	—	—	—	—	—	—	—	—	—

Lac		Ottsjön																									
Date		14.8.50				15.8.50				17.8.50				21.8.50													
Station	Prof.	A	A	A	A	M	M	N	N	O	O	A	A	A	A	F	E	E	E	X	Y	Ä	Ä	Ä	Ä	Z	Z
Heter. s. ad.		1	3	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1								
Holop. gibb.		1				1	1	1	1	1	1	1	2	1					1						1		
Byotr. l. . . .										1																	
Chydoridae.																											
Cy. cop.															1								1	1			

Lac		Ottsjön																									
Date		21.8.50				22.8.50				25.8.50				26.8.50													
Station	Prof.	A	B	C	D	A	A	C	C	C	D	D	D	A	A	A	A	A	A	B	B	B	D	D	D	C	C
Heter. s. ad.		3	3	3		1	2	2					1	1	1	1	4	2	2	1	3	1	5	1	4		
Holop. gibb.			1			1	1	1	2	1	1	1		1	1			1					2	1			
Polyph. ped.					2																						
Byotr. l. . . .									1											1							
Chydoridae.					8																						
Cy. cop.					4																						

Lac		Ottsjön																														
		26.8.50				28.8.50				30.8.50				11.8.51				15.8.51				20.8.51										
Date	Station	A	B	C	D	D	A	A	B	C	D	A	A	A	A	C	C	C	D	D	C	D	A	C	D	D	A	A	C	D	D	
Prof.	Prof.	0	0	0	0	15	0	0	0	0	0	0	2	5	10	15	0	2	15	0	10	0	2	2	24	29	10	20	26	2	15	20
Heter. s. ad.		3	3	3	1		3	3	3	1	1																					
Holop. gibb.							1	1	1	1	1		1	1	1	3	1	3	1	1												
Bytoir. l.																																
Cy. cop.						1																										

Lac		Ånn																																					
		31.3.46				6.6.46				13.7.46				16.8.46				1.10.46				7.5.48				23.8.48													
Date	Station	A	A	A	A	A	A	A	A	G	F	F	F	B	A	A	A	E	E	E	E	C	C	C	C	C	C	C	C	C	C	C	C	C	C				
Prof.	Prof.	1	5	10		5	10			0	0	0	0	0	15	10		1	1	1	1	0	0	0	0	0	0	0	0	5	5	5	5	5	5	5	5	5	5
Diapt. dent. .																																							
Heter. s. ad.																																							
Heter. s. co.																																							
Holop. gibb.		2	1	4						5	5	5				1																							
Polyph. ped.										1	5																												
Bytoir. l.																																							
Chydoridae .																																							
Cy. cop.														3	2																								

Index bibliographique

- AURICH, H. 1934. Mitteilungen der Wallacea Expedition. *Zool. Anz.* 108: 59—74.
- BANTA, A. M. 1939. Studies on the physiology, genetics and evolution of some Cladocera. *Publ. Carneg. Instn.* 513: 1—285.
- BERG, K. 1934. Cyclic Reproduction, Sex Determination and Depression in the *Cladocera*. *Biol. Reviews IX (2)*: 139—174.
- 1936. Reproduction and Depression in the *Cladocera* illustrated by the Weight of the Animals. *Arch. Hydrobiol.* XXX: 438—462.
- BONNIER, G. et TEDIN, O. 1940. Biologisk variationsanalys. Stockholm.
- BRUNDIN, L. 1942. Zur Limnologie Jämtländischer Seen. *Rept. Inst. Freshwater Res. Drottningholm (Medd. Statens Unders. Försöksanst. Sötvattensfisket)* 20: 1—104.
- BURCKHARDT, G. 1899. Faunistische und systematische Studien über das Zooplankton. *Rev. Suisse Zool.* 7: 680—683.
- 1910. Hypothesen und Beobachtungen über die Bedeutung der vertikalen Planktonwanderung. Nachtrag. *Int. Rev. Hydrobiol.* III: 156—172, 335—338.
- 1941. Esistono forme intermedia fra »le due specie de *Bosmina*»? *Zeitschr. Hydrol., Schweiz. Nat.forsch. Gesellsch.* IX: (1—2): 128—148.
- CLAUS, C. 1857. Das Genus *Cyclops* und seine einheimischen Arten. *Arch. f. Nat. gesch.* XXIII (1): 1—40.
- 1895. Wiederbelebung im Schlamme eingetrockneter Copepoden und Copepodeneier. *Arb. Zool. Inst. Wien* 11: 1—12.
- COKER, R. E. 1933. Influence of Temperature on Size of Freshwater Copepods (*Cyclops*). *Int. Rev. Hydrobiol.* 29 (5/6): 406—436.
- 1934. Influence of Temperature on Form of the Freshwater Copepod, *Cyclops vernalis*. *Int. Rev. Hydrobiol.* 30 (5/6): 411—427.
- 1939. The Problem of Cyclomorphosis. *Quart. Rev. Biol.* 14: 137—148.
- CUSHING, D. H. 1951. The vertical Migration of Plankton. *Biol. Rev.* 26: 158—192.
- DIETRICH, W. 1915. Die Metamorphose der freilebenden Süßwassercopepoden. *Zeitschr. wiss. Zool.* 113: 252—324.
- EKMAN, S. 1904. Die Phyllopoden, Cladoceren und freilebenden Copepoden der nord-schwedischen Hochgebirge. *Zool. Jahrb. Abt. Syst.* 21 (1): 1—170.
- 1907. Über das Crustaceenplankton des Ekoln . . . Zoologiska Studier tillägnade professor Tullberg, 42—65. Uppsala.
- 1922. Djurvärldens utbredningshistoria på Skandinaviska halvön. Stockholm.
- FINDENEGG, I. 1943. Untersuchungen über die Ökologie und die Produktionsverhältnisse des Planktons im Kärntner Seengebiet. *Int. Rev. Hydrobiol.* 43 (4/6): 368—429.
- FREIDENFELT, T. 1925. Bemerkungen über die Bedeutung und die Methoden einen mathematischen Prüfung von Mittelwerten. *Abderhalden, Handbuch IX (2)*.
- GURNEY, R. 1929. Dimorphism and rate of growth in *Copepoda*. *Int. Rev. Hydrobiol.* 21: 189—207.
- HAECKER. 1902. Über das Schicksal der elterlichen und grosselterlichen Kernanteile. Jena.
- HUITFELDT KAAS, H. 1906. Planktonundersøgelser i Norske vand. Christiania.
- KIKUCHI, K. 1930. Diurnal migration of plankton *Crustacea*. *Quart. Rev. Biol.* 5: 189—206.
- KOFOID, C. A. 1903—1908. The Plankton of the Illinois River. *Bull. Illinois State Lab.* VI, VIII.
- LANGFORD, R. R. 1938. Diurnal and Seasonal Changes in the Distribution of the Limnetic *Crustacea* of Lake Nipissing, Ontario. *Univ. Toronto Stud. Biol. Ser.* 45: *Publ. Ontario Fish. Res.* 56: 1—142.
- LIEDER, U. 1950. Beiträge zur Kenntnis des Genus *Bosmina* I. *Arch. Hydrobiol.* XLIV (1): 77—122.

- LINDSTRÖM, T. 1949. Etude quantitative des Planctons Crustacées dans quelques lacs du Jämtland. *Rept. Inst. Freshwater Res. Drottningholm*. 29: 51—56.
- LOHAMMAR, G. 1938. Wasserchemie und höhere Vegetation schwedischer Seen. *Symbolae Botan. Upsalienses III*. 1—252.
- LOWNDES, A. G. 1929. Result of breeding Experiments and other Observations on *Cyclops vernalis* and *Cyclops robustus*. *Int. Rev. Hydrobiol.* 21: 171—188.
- MAC KAY, H. H. 1951. The Net Plankton of Lake Nipigon. Thesis. Univ. Toronto. P. 1—4.
- MAYR, E. 1949. Speciation and Systematics. P. 281—298. Jepsen, Simpson, Mayr: Genetics, Paleontology and Evolution. New Jersey.
- OLOFSSON, O. 1918. Studien über die Süßwasserfauna Spitzbergens. *Zool. Bidrag Uppsala* 6: 181—648.
- OHLE, W. 1940. Chemischer Gewässererkundung in Schwedisch-Lappland. *Arch. Hydrobiol.* 36 (3): 337—358.
- OSTWALD, W. 1902. Zur Theorie des Planktons. *Biol. Centralbl.* 22: 596—605, 610—638.
- PENNAK, R. W. 1944. Diurnal Movements of Zooplankton Organisms in some Colorado Mountain Lakes. *Ecology* 25 (4): 387—403.
- PLEW, W. F. et PENNAK, R. W. 1949. A Seasonal Investigation of the Vertical Movements of Zooplankters in an Indiana Lake. *Ecology* 30 (1): 93—100.
- REIF, C. 1939. The effect of stream conditions on lake plankton *Trans Amer. Micr. Soc.* 58 (4): 398—403.
- RICKER, W. E. 1937. Statistical Treatment of Sampling Processes useful in Enumeration of Plankton Organisms. *Arch. Hydrobiol.* 31 (1): 68—84.
- 1938. On Adequate Quantitative Sampling of the Pelagic Net Plankton of a Lake. *J. Fisc. Res. Board Canada IV* (1): 19—32.
- RODHE, W. 1941. Zur Verbesserung der quantitativen Planktonmethodik. *Zool. Bidrag Uppsala* 20: 465—477.
- 1949. The ionic composition of lake waters. *Verhandl. Int. Verein. Limnolog.* X: 377—386.
- ROY, J. 1932. Cité par WESENBERG-LUND, C. 1937. Ferskvandsfaunaen biologisk belyst. København.
- RUTTNER, F. 1909. Über tägliche Tiefenwanderungen von Planktontieren unter dem Eise und ihre Abhängigkeit vom Lichte. *Int. Rev. Hydrobiol.* 2: 396—423.
- 1914. Uferflucht des Planktons und ihre Einfluss auf die Ernährung der Salmonidenbrut. *Int. Rev. Hydrobiol. Suppl. Biol.* 6: 1—7.
- 1930. Das Plankton des Lunzer Untersees. *Int. Rev. Hydrobiol.* 23: 1—287.
- 1940. Grundriss der Limnologie. Berlin.
- 1943. Beobachtungen über die tägliche Vertikalwanderung des Planktons in tropischen Seen. *Arch. Hydrobiol.* XL (2): 474—492.
- RYLOV, W. H. 1935. Das Zooplankton der Binnengewässer. Die Binnengewässer XV. Stuttgart.
- SARS, G. O. 1903, 1918. An Account of the *Crustacea* of Norway. IV, VI. Bergen.
- SCOURFIELD, D. J. et HARDING, J. P. A key to the British Species of Freshwater Cladoceres. *Freshwater Biol. Assoc. Brit. Empire, Scient. Publ.* 5: 1—50.
- SOUTHERN, R. et GARDINER, A. C. 1926. The Seasonal Distribution of the *Crustacea* of the Plankton in Lough Derg and the River Shannon. *Departm. Fish. Scient. Invest.* 1 Dublin: 1—170.
- 1932. The Diurnal Migrations of the *Crustacea* of the Plankton in Lough Derg. *Proceed. Roy. Irish Acad.* XL, Sect. B, (11): 121—159.
- Thomasson, K. 1951. Beiträge zur Kenntnis des Planktons einiger Seen im nordschwedischen Hochgebirge. *Schweiz. Zeit. Hydrol.* XIII: 336—351.

- TONOLLI, V. 1949 a. Ciclo biologico, isolamento e differenziamento stagionale in popolazioni naturali di un *Copepoda* arbitratore di acque alpine. *Memoire dell'Istituto Ital. di Idrobiol.* V: 95—144.
- 1949 b. Struttura spaziale del popolamento mesoplanctico. *Ibid*: 189—208.
- 1949 c. Ripartizione spaziale e migrazioni verticali della zooplankton. *Ibid*: 209—228.
- WAGLER, E. 1927. Über die »Schwebeforsätze« der Daphnien. *Zool. Anz.* 74: 284—302.
- WALTER, ELISABETH. 1922. Über die Lebensdauer der freilebenden Süßwasser-Cyclopoiden und andere Fragen ihrer Biologie. *Zool. Jahrb. Abt. Syst.* 44: 375—420.
- VANDEL, A. 1919. Contribution à la connaissance des eaux douces de Jura. *Bull. Soc. Zool. France XLIV.*
- WESENBERG LUND, C. 1926. Contribution to the Biology and Morphology of the Genus *Daphnia*. *Kongl. Danske Vidensk. Selsk. Skrifter. Række 8. Nat.-mat. afd.* 11: 89—252.
- VIVIER, P. 1937. Sur les variations quantitatives du plancton pélagique du lac du Bourget. *Trav. Assoc. Intern. Limnol.* VIII (1): 55—108.
- WOLF, E. 1904. Dauereier und Ruhezustände bei Kopepoden. *Zool. Anz.* 27: 98—108.
- WOLTERECK, R. 1908. Plankton und Seeausfluss. *Int. Rev. Hydrobiol.* I: 303—304.
- 1921. Variation und Artbildung. *Ibid IX*: 1—152.
- 1926. Notizen zur Biotypenbildung der Cladoceren I. *Ibid. XIV*: 121—127.
- 1928 a. Über die population Fredriksborger Schloss-See. *Ibid. XIX*: 172—203.
- 1928 b. Über die Spezifität des Lebensraumes der Nahrung und der Körperformen bei pelagischen Cladoceren. *Biol. Zentralbl.* 48 (9): 521—551.
- WORTHINGTON, E. B. 1931. Vertical Movements of Freshwater Macroplankton. *Int. Rev. Hydrobiol.* XXV: 394—436.

Beitrag zur Fauna einiger Wasseransammlungen in der Balsberggrotte

Von HEINZ LÖFFLER

Anlässlich meines Aufenthaltes an der hydrobiologischen Station Aneboda, August 1951 hatte ich u.a. auch zu einem kurzen Besuch der Balsberggrotte Gelegenheit. Ueber das Ergebnis der Untersuchung einiger dort mit dem Planktonnetz entnommener Proben sei hier berichtet. Für einen Arbeitsplatz im Seelabor von Aneboda habe ich Herrn Prof. S. THUNMARK zu danken, Herrn Dr. BERZINS, der mir bei der Bestimmung vor allem der *Bdelloidea* behilflich war, bin ich zur Dank verpflichtet.

Die vor allem den Geologen und Paläontologen bekannte Grotte in Nordostschonen am Fuss des Balsbergs, westlich vom Råbelöv-see ist durch Auflösen des der oberen Kreide angehörenden Kalksteins entstanden und wurde durch nunmehr längst eingestellten Kalkbruch vergrößert. Einer mündlichen Mitteilung Herrn Dr. LINDBERGS, Lund, zufolge wären in den letzten Jahren Teile der Grotte eingestürzt und ein Abschnitt derselben unbetretbar. Einige kurze Seitenstollen der durch Fossilien (besonders Belemniten) berühmten Grotte stehen unter Wasser, das teilweise über einen Meter tief war und folgende, quantitativ sehr spärlich vertretene Fauna enthielt.

Neben verhältnismässig zahlreichen Difflugien und anderen beschaten Rhizopoden waren die *Protozoa* vertreten durch:

<i>Stylonichia mytilus</i> EHRBG.	(insges. 5 Tiere)
<i>Oxytricha</i> sp.	(» 1 »)
<i>Trachelius ovum</i> EHRBG.	(» 1 »)
<i>Lionotus</i> sp.	(» 1 »)

Von den Heliozoen lag ein Exemplar vor: *Actinosphärium* sp.

Nematoda (insges. 3 Tiere)

Von den Rotatorien sind vor allem *Mniobia scarlatina* EHRBG. zu erwähnen. Die Zähnezahzahl betrug 7/7, der Darm hatte eine auffallend rotbraune Färbung, wie sie für diese Art charakteristisch ist. Ferner *Rotaria elongata* WEB. Beide nur durch ein Tier vertreten,

<i>Lecane luna</i> EHRBG.	(insges. 3 Tiere)
<i>Lecane closterocerca</i> SCHMARDA	(» 1 »)
<i>Colurella adriatica</i> EHRBG.	(» 1 »)

Nach einer mündlichen Mitteilung von Dr. LINDBERG, Lund, wurden ausser Cyclopiden auch noch Harpacticiden und Ostrakoden beobachtet. Die Proben von 26.8.1951 enthielten jedoch nur 2 Nauplius- und 1 Copepoditstadium (♂) wahrscheinlich einer *Cyclops*-art.

Die Armut an Lebewesen dieser kleinen Grottengewässer ist wohl zum grössen Teil, wenn nicht überhaupt auf Lichtmangel zurückzuführen, doch wäre in diesem Zusammenhang eine Analyse des Wassers selbst wünschenswert. Auch würden Probenentnahmen im Laufe eines Jahreszyklus sicher von Interesse sein, nicht nur in ökologischer Hinsicht, sondern auch, um die gesamte Fauna erfassen zu können.

Pike-perch studies in Lake Vänern

By CARL PUKE

Introduction

In Vänern, the largest lake in Sweden with an area of 5,550 km², there is considerable fishing especially for burbot, pike, pike-perch, perch, vendace, whitefish, trout and salmon. The pike-perch plays an important role and the yield from this fish seems to have increased to such an extent during the course of the years, that pike-perch is probably among the three or four foremost species of fish as regards profit (Table 1.)

Table 1. The yield from fishery in Lake Vänern according to Törnquist 1941.

Species	Yield in kg.	
	Year 1914—1923 (average)	Year 1936
Burbot	170.500	302.000
Pike	126.500	184.000
Pike-perch	50.500	177.500
Perch	116.500	155.000
Vendace	77.500	109.000
Whitefish	61.000	100.500
Salmon Trout	23.000	21.500
Other species	169.000	139.500
Total	794.500	1.242.500

Some Principal Features of the Pike-perch's Conditions of Life and Pike-perch Fishery in Lake Vänern

The pike-perch spawns at several places in Lake Vänern, only a few of which, however, are of any greater consequence. The following are the most important, those of greatest consequence being placed first. Their situation may be seen in the map (Fig. 1.).

1. *The Kristinehamn area* with Ölme and Varnumsviken with Vålösund near Kristinehamn.
2. *The Detter area* with Brandsfjorden in the south near Vänersborg.
3. *The Kållandsö area* (Ullersund) in the neighbourhood of Lidköping.

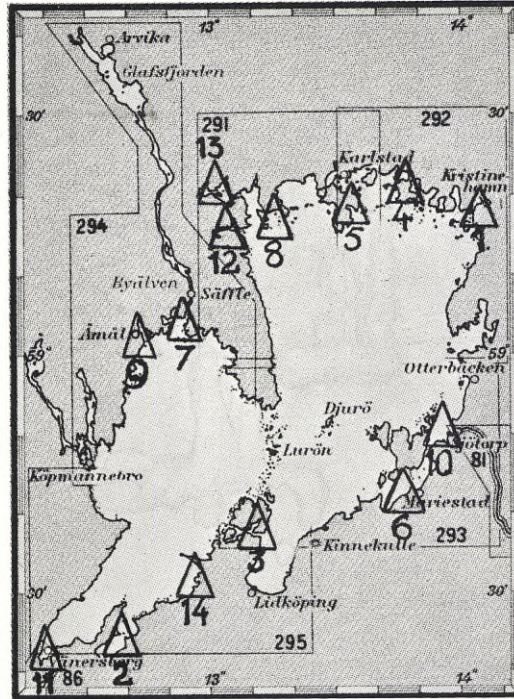


Fig. 1. The most important spawning-grounds for pike-perch in L. Vänern.

\triangle = spawning-ground for pike-perch,
number refers to designation in text.

4. *The Arnö area* with Bottviken and Arnöfjorden between Kristinehamn and Karlstad.
5. *The Hammarö area* with the Jäverö area near Karlstad.
6. *The Mariestad area* near Mariestad.
7. *The Byälva area* near Säfte.
8. *The Segerstad area* near Åsundaön SW of Karlstad.
9. *The Åmålsvik area* near Åmål.
10. *The Sjötorp area* with the Börstorp area north of Mariestad.
11. *The Vassbotten area* near Vänersborg.
12. *The Kyrkebysjö area* rather far SW of Karlstad.
13. *The Grumsfjord area* with Borgvikssjön W of Karlstad.
14. *The Söne area* NW of the Detter area and Vänersborg.

Within the areas listed above the pike-perch goes in to spawn in the spring and is then caught mainly in fyke-nets or basin fyke-nets but also in nets. During the wintertime the pike-perch seems to stay out in deeper water and there are considerable winter catches in nets along the eastern side of the wide spread Luröarchipelago, south of Hammarön and off the coast south of Kristinehamn. In addition fishing is carried on with otters in the summer, quite a lot of pike-perch being caught. Such fishing takes place over the entire



Fig. 2. The Dettar area and recaptures of pike-perch marked there.

● = recovery.

lake in Dalbosjön between Säffle and Vänersborg and Kinnevik, the bay N from Lidköping, while the otter fishermen in the deeper waters of Northern Vänern in Värmlandssjön between Karlstad and Djurö as a rule keep nearer land (see Fig. 1.)

The Kristinehamn area in Northern Vänern and the Dettar area in the south were selected for study.

The Dettar Area

The Dettar area partly consists of Dettarn Bay lying furthest in, partly of Brandfjorden lying outside as well as the adjoining water area in Vänern in Dalbosjön. (Fig. 2.) The sound between Dettarn and Brandfjorden is called Frugårdssundet. Dettarn, which constitutes the real spawning bay, is 30 km² in size. The depth is insignificant and usually amounts to between 1.5—2 m. It is greater (3.5 m) in Brandsfjorden. The water level in Lake Vänern varies rather considerably from year to year. In years with high water the average depth in Dettarn is 2—2.5 m.

As long as there is no ice-covering, the water layers are well mixed and the temperature of the water corresponds rather closely to that of the air. As far as the oxygen content is concerned, it too seems to be high through

Table 2. Hydrographic particulars from Dettern; obtained from samples 12/5 1948.

	West side (1.7 m depth)			Middle of lake (1.6 m depth)			East side (1.5 m depth)		
	Temp °C	O ₂ mgl	pH	Temp °C	O ₂ mgl	pH	Temp °C	O ₂ mgl	pH
surface ...	16.8	10.71	7.3	16.3	10.54	7.2	16.0	10.54	7.2
1 m.	16.8	11.11	—	16.3	10.59	—	16.0	10.76	—
at bottom	16.8	10.54	7.2	16.3	10.59	7.2	15.8	11.11	7.2

Table 3. Hydrographic particulars from Dettern; obtained from surface water samples, wind NW. 12/5 1948.

	West side	Middle of lake	East side
Depth of visibility	0.17	0.13	0.12
Carbonic content mgl. CO ₃	24	—	24
Electronic conductivity χ_{18}° n · 10 ⁻⁶	103	—	105
Electrolyte content mgl.	77	—	79

the entire mass of water (Tables 2 and 3.) Shores and bottom in the south-eastern part mainly consist of clay, which is carried into the water and mixed with it. Depth of visibility is, therefore, very slight and can in windy weather amount to only about a decimeter. Where the stream Nossan runs in to the east, the water becomes clearer, however, depending on the water in the stream being less mixed with clay. Vänern water flowing in with northerly winds also increases the depth of visibility appreciably (Table 4).

The pre-requisites in Dettern as a spawning-ground for pike-perch thus seem to be the best possible. Spawning seems first and foremost to take place in the southeastern parts, where the water is most markedly mixed with clay. Here the bottom consists of firm clay in which stones and gravel are inbedded, here and there overgrown with *Litorella*. The bottom of the central parts is soft and consists mainly of clay mud, which scarcely provides a suitable ground for spawning.

Spawning migration begins when the ice breaks up, which usually occurs in the middle or end of April. The entrance is facilitated by a special channel being staked out in Furugårdssundet, no fishing tackle being allowed to be laid out in the channel. After the spawning season, which broadly speaking is usually concluded about May 20th, a great number of the pike-perch seems to move back out into Lake Vänern. In any case, the catches after spawning are very small, which indicates an emigration from the area.

Pike-perch fishing in Dettern takes place mainly during the spawning season. Fyke-nets and nets are then used. The fyke-nets represent a small type and the height of the largest bow amounts to 1.2 m and the length of the

Table 4. Hydrographic conditions of surface water in Dettern with NE wind 10/5 1948.

Locality	Depth of visibility	Temp °C	pH	$\alpha_{18}n \cdot 10^{-6}$	Electrolyte content mg/l
At Frugårdssundet	0.46	15.0	7.0	99	74
Outside the mouth of Nossan	0.36	15.0	6.9	102	76
In Southern section by eastern shore	0.20	15.5	7.3	105	79
In Southern section by western shore	0.12	17.2	7.2	103	77

entire tackle is about 8 m, 4.5 m of which being the two arms, which are turned to face land when fishing. They are usually set out in rows, more or less at right angles to the shore and lie for the greater part in an east-westerly direction. Every such row is divided up in a number of links. In every link there are usually 12 fyke-nets and the length of such a link is 100 m. The links are separated by an interval of 30 meters. As a rule not more than 5—7 links are placed in a row. This method of arranging the nets prevents the pike-perch's passage from being closed. It has access to the entire bay in spite of the tackle. The total number of fyke-nets amounts on an average to 1,850 every year.

Apart from this fyke-net fishery, net-fishing also occurs with a varying number of nets. At present such net-fishing is, however, forbidden from April 24th to May 10th.

During the rest of the year some pike-perch is caught, though on a very small scale compared with the spring fishing.

In addition to Dettern, pike-perch is caught in Brandsfjorden and in the water out in Vänern adjoining the area. This fishing is mainly with nets. A great deal of pike-perch is captured under the ice before the break-up especially along the shores outside the area.

The Vålösund Area

The part of the Kristinehamn area, which was the subject of investigation, consists of Varnumsviken with the sound leading to it, Vålösund, and the water adjoining it out in Vänern. The topographical conditions differ quite considerably here from those in the Detter area (Fig. 3). The entrance sound, Vålösund, is a long narrow sound about 4 km long and 5 m deep in the middle channel in to Varnumsviken, where spawning takes place. Varnumsviken is a rather deep bay up to 9 m in depth. The water is quite clear and not particularly clouded. The great depth results in rather definite layers

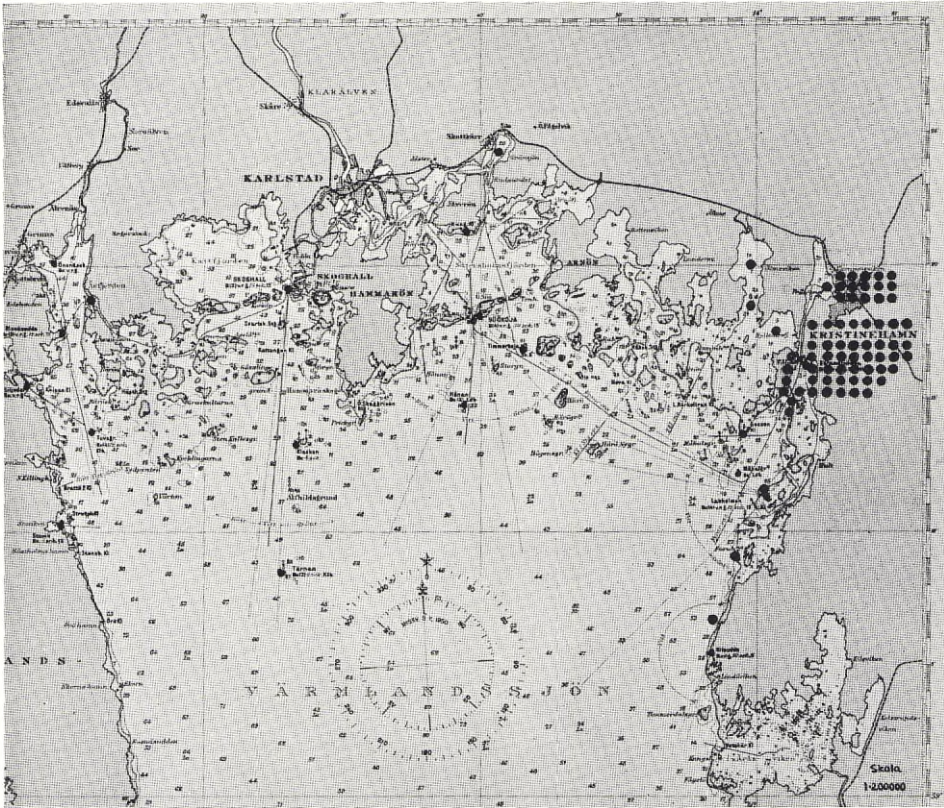


Fig. 3. The Vålösund area and recaptures of pike-perch marked there.

● = recovery. × = locality for marking in Vålösund.

being formed here, both as regards temperature and oxygen content, with low figures for the temperature and oxygen content even quite early in the spring (Table 5). A contributory factor to the low oxygen content at the bottom also seems to be the fact that the town of Kristinehamn releases large quantities of waste water into the bay, which moreover, at Vålösund constitutes the general fairway with extensive traffic including ocean-going vessels.

The most important spawning-ground seems to be the so-called Prästerudsudden, a bank with clay, sand, gravel and stone as well as mud projecting outwards from the east, where Varnumsviken merges into Vålösund. Spawning takes place along the western shore as well and in the most northerly part of the bay. Fishing for pike-perch within the area occurs almost entirely with large basin fyke-nets. The majority of them are set out in the outer half of Vålösund and along the eastern side of Valön. There are fewer inside Varnumsviken. In the sound they are set out along the

Table 5. Hydrographic particulars from Varnumsviken, obtained from samples May 29th 1947.¹

Depth m	Prästerud reef			Deep area outside the reef		
	Temp °C	O ₂ mg/l	pH	Temp °C	O ₂ mg/l	pH
surface.....	20.6	11.58	7.0	20.0	12.13	
1	18.9	9.85				
2	18.1	9.41				
3				17.0	6.86	
4	16.5	5.45	6.3			
5	bottom			14.2	5.37	
6						
7.5.....				13.5	3.12	
8.5.....				12.5	2.80	6.3
				bottom		

¹ The depth of visibility was 1.0 m and the carbonic content 13 mg/l at surface, 18 at 4 m depth and 22 mg/l at 7 m depth.

shores with the arms turned to face land, as a rule with only one or two fyke-nets in the same row. The most usual depth for them is 4.2 m and the length 30 m, about 15 m of which being the three arms, a middle arm and two side arms. The number of such basin fyke-nets set out in the area every year amounts on an average to 180.

Net-fishing is carried on primarily outside Vålösund in the entrance area and out in Lake Vänern. The greater part of the catch is taken during the spring from May to June, pike-perch fishing during the remainder of the year being inconsiderable as compared with the spring catch.

The Result of Marking Pike-perch in Lake Vänern

Pike-perch marking has been carried out in Lake Vänern partly in the Detter area and partly in the Vålösund area. The fish marked in the Detter area were small pike-perch inside Dettern. The average length of the fish used was 38 cm. These markings were made by Fishery Assistant P. HJORTH in the spring of the years 1946—1949. The writer marked a number of larger pike-perch with an average length of 50 cm, in the spring of 1948.

In Vålösund marking was done during the autumn of the years 1947, 1948 and 1949 by Mr. HJORTH and by myself in the spring of 1949. The fish then used had an average length between 45—50 cm. Altogether 482 pike-perch were marked, of which 242 were in Dettern and 240 in Vålösund. Up to the present 107 recaptures have been reported, 33 of which were in the Detter area (14 %) and 74 in Vålösund (31 %).

A closer survey of the recaptures, a detailed summary of which may be found in table 6 as well as in figs. 2 and 3, gives the following results.

In the Dettern area 14.8 % of the fish marked in May 1946 were recaptured partly during the spring fishing the same year but also during the following two years, in addition to which two specimens were caught during winter fishing with nets in 1949. All of these were captured inside Dettern or in Brandsfjorden apart from one, which was caught in a net in April 1947 at Friel, where extensive fishing with nets takes place during the time preceding migration into Dettern for spawning. Pike-perch marked in June the same year have not yielded any recaptures, which probably is due to unsuitable marking conditions. The warmer water at that time gives the pike-perch poorer powers of resistance to marking and these pike-perch may have died soon after being marked.

The marking in 1947 gave all the recaptures the following year with the exception of one, which occurred next year during the spring fishing in Dettern. Two of the others were caught during winter fishing out in Vänern, the remainder in Dettern or Brandsfjorden. Altogether 18.6 % of the marked pike-perch were recaptured.

During the year 1948 the marking of larger pike-perch resulted in 23.2 % being recaptured, this mainly taking place during the spring fishing in Dettern the same year. One recapture is reported, however, from the autumn fishing out in Lake Vänern. The smaller pike-perch recaptured amounted to 11.1 %, three fishes being caught out in Vänern the same autumn, while the remainder were caught in Dettern, one as late as the spring fishing in the year 1951.

The last year marking occurred, 1949, results were poor. Only one fish was reported as being recaptured during the spring fishing in Dettern that year of the 39 pike-perch marked.

The majority of recaptures (80 %) have, consequently, been made in Dettern while fishing out in Lake Vänern has yielded 18 %, in addition to which one recapture was made on the coast further east. No long distance finds have been reported.

The greater number of the fish marked in Vålösund in the autumn of 1947 were recaptured during the spring fishing at the same locality in 1948. Altogether 20,6 % were recovered. One was caught as late as the spring of 1951. Recoveries have also been made partly inside Vålösund and in Varnumsviken, but also out in Vänern to the south at Medhamn (18 km, one) and at Lakholmen (12 km, one) in December 1948. In addition one of the marked pike-perch had gone as far as the Skattkärr area. The place, where it was recaptured, lies 26 km from the locality at which the fish were released. The recapture was made in May 1948.

The majority of the pike-perch marked in September 1948 were recovered during the spring fishing in 1949, but quite a number were recaptured as well during the autumn fishing the same year and the following spring. No less than 36.8 % have been reported. The greater part of them were

Table 6. Marking and recapture of pike-perch in Vänern during the years 1946—1951.

Locality for release	Marking			Recapture										Total recapture	Percentage of recapture	
	Date	Number	Type	1946 ¹	1947		1948		1949		1950		1951			
				Spring	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn		
Detttern	May 1946	54	small pike-perch	3	1		2	2							8	14.8
	June 1946	10	»												0	0
	May 1947	43	»				5	2	1						8	18.6
	April 1948	43	large				8	1	1						10	23.2
	May 1948	53	small				1	3	1					1	6	11.1
May 1949	39	»						1						1	2.6	
Detttern Total		242		3	1	—	16	8	4	—	—	—	1	—	33	14.0
Välösund	September 1947	34	large pike-perch				5	1				1			7	20.6
	September 1948	60	»					3	11	5	3				22	36.8
	May 1949	80	»						33	1	3				37	46.4
September 1949	66	»							3	4			1	8	12.2	
Välösund Total		240		—	—	—	5	4	44	9	10	1	1	—	74	30.8

¹ Spring = fishing during April—June.² Autumn = fishing during July—March.

caught in Vålösund or in Varnumsviken. One recapture was reported from Vänern at Furholmarna 14 km to the south. It was made in December 1949. One fish was also caught in Ölmeviken, belonging to the Kristinehamn area, in May 1949, and yet another specimen at the same place in June 1950.

The fish marked in the spring of 1948 were recaptured for the greater part during the spring fishing the same year in Vålösund, that is to say during the time the marking was being undertaken. One recovery was reported from the adjoining Hjälmarsfjorden in August 1949. The rest were reported during the spring fishing in 1950 in Varnumsviken or in the water at Vålösund. The percentage of recaptures was very high amounting to 46.4 %, obviously depending on the fact that marking took place at the same time as the intensive spring fishing.

Finally as far as the marking in 1949 is concerned, recaptures were mainly reported from the autumn fishing in 1949 but also from the spring fishing 1950. Recoveries were made in Vålösund or in Varnumsviken. One recapture was reported from the Segersta area, the locality for recovery being 48 km from the locality where marking took place. This recapture was made in November 1949. Altogether 12.2 % of the marked fish were recovered.

By far the greater part of the recaptures were made in Vålösund (66 %), Varnumsviken coming next with 22 %. Recoveries within the water area adjoining the marking area amounted to 9 %, and outside the same area there were only 2 recoveries.

SVÄRDSON (1948) found a tendency towards rather extensive migrations in the pike-perch of Lake Mälaren. His material was small, however, due to very low percentage of recapture.

The greater number of recaptures in Vänern have been made within the spawning areas. It seems, therefore, to be definitely confirmed, in any case in the areas investigated, that the pike-perch, which can be caught by ordinary fishing, return to a great extent for spawning to the place where they spawned before. Recoveries of any significance have not occurred in the spawning-grounds adjoining the areas investigated or in any other places, which should be the case if confinement to one spawning-ground was less pronounced.

The evidence for long migrations made to and from the spawning-grounds by the pike-perch is small. It can be safely said, however, that it spreads to the water areas adjoining the spawning areas. Bearing in mind the few recoveries made outside the spawning-grounds (8 in Vålösund and 7 in Dettern), it is probably still too early to say anything with certainty as to whether actual long general migrations really occur regularly. It may be noted, however, that in the Detter area no distant recoveries were made and in the Vålösund area only two.

Acknowledgements

I should like to express my sincere gratitude to Fishery Assistant P. HJORTH, Mariestad, Mr. ALBIN ARONSON, Kristinehamn, Mr. CARL MARS, Lilleskog and Mr. ANDERS SAHLBACK, Salstad who have given kind assistance and support to the study.

References

- TÖRNQUIST, N. 1941. Fiskets avkastning i Vänern. *Svensk Fiskeri Tidskrift* 50: 129—134.
SVÄRDSON, G. 1948. Ett gösmärkningsförsök. *Svensk Fiskeri Tidskrift* 57: 173—174.

The Population of Trout, *Salmo trutta*, LINNÉ, in Regulated Lakes

By SVEN RUNNSTRÖM

Introduction

In the North Swedish rivers the water flow is very high in the spring and summer, while it decreases considerably later on during the winter. The power stations built up in the rivers have, consequently, the poorest supply of water during the season when the demand for electric power is greatest. The electric power companies have, therefore, regulated the lakes to a great extent by means of dams and they store the water here during the summer, so as to be able to let it out during the autumn and winter.

In the Järpströmmen water system, one of the upper tributaries of the River Indalsälven, a group of lakes have been regulated, which were taken into use during the years 1937—1940 and the Laboratory has observed the effect of the regulation on the fish populations here. I have dealt with the char population in one of these impounded lakes, Torrön, in a previous paper (RUNNSTRÖM 1951). The char spawn in the lake on the stony bottom by the shores or on reefs out in the lake and owing to variations in the water level these spawning-grounds are partly drained in the winter, causing some of the spawn to be destroyed. In the present work an account is given of the result of the regulation on the brown trout population, which — as opposed to the char in these lakes — has its spawning-grounds and localities for growth in the streams and is, therefore, affected by the interference with their water flow.

The Area and Material Investigated

The system of lakes investigated comprises five lakes (Fig. 1). The largest lake, Kallsjön, is fed partly by Rensjön and Anjan through the streams Rensjöån and Sundströmmen partly by Torrön and Juveln through the streams Ängströmmen and Kallströmmen. Kallsjön drains through Järpströmmen into the main river, Indalsälven. All the lakes are regulated by means of dams in the outlet rivers. A power station has been built by the barrage in Järpströmmen below Kallsjön and a great number of power stations have also been built further down the Indalsälven. By the regulating

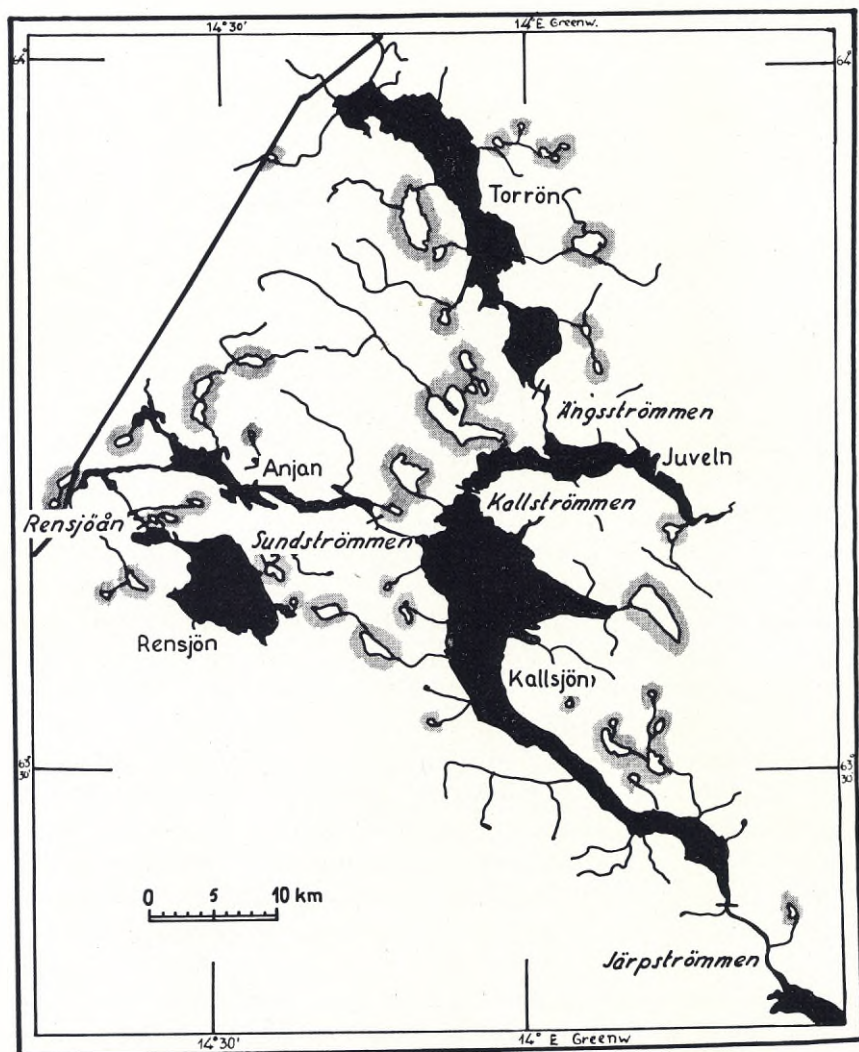


Fig. 1. The investigated area.

dams lowering canals have been dug in the rivers, so that the water level in the lakes could even be reduced below the natural low water level.

Table 1 shows the height of the lakes above sea level and their area. It may also be seen that Torrön was the first lake to be regulated in the year 1937, this regulation being extended in the year 1940 to comprise a regulation height, that is to say the difference in height between the lowering and damming limits, of 12.85 meters and a storage capacity of 1,221 million m^3 . The remaining lakes were regulated 1940, but have smaller regulation heights and storage capacities than Torrön.

Table 1. Regulations of the lakes.

Lake	Regulated in the year	Height above sea level m.	Area km ²	Height of regulation, m.	Magazine volume mill. m ³
Rensjön	1940	501	47	1.80	85
Anjan	1940	420	26	9.20	239
Torrön	1937—40	411	95	12.85	1.221
Juveln	1940	393	36	8.55	308
Kallsjön	1940	381	155	3.65	566

As may be seen in table 2, trout, char and burbot are to be found in all the lakes. Grayling only exists in Kallsjön, Juveln and Torrön, but has been illegally introduced into Anjan during the last few years. Whitefish is only found in Kallsjön, where it was transplanted approximately 30 years ago. In this lake there are also roach and minnows, but they are, however, of no economic importance.

Before the regulation the trout could probably migrate up through Kallströmmen to Juveln with certain water levels and in Ängströmmen it had free passage up to Torrön. In Sundströmmen and Rensjöån just above its outflow into Anjan, there are such high falls, that the fish have not been able to pass them.

The trout populations in the lakes have primarily been controlled by test fishing with nets, carried out by the staff of the Laboratory during the summer. Scale samples have been taken and the length and weight of the fish have been recorded. This test fishing could be commenced a little while before the regulation with the exception of Torrön, where the investigations were first started the year after the lake was impounded. Test fishing has been carried on since then with a few interruptions up to 1951. All fishing is prohibited in the rivers during the spawning season after September 1st and no particulars concerning the spawning populations are available with the exception of two streams, Rensjöån and Kallströmmen. In the Rensjöån the spawning migration has been controlled by means of a fish ladder since the years 1946 (RUNNSTRÖM 1949), and in the Kallströmmen the regulation association has carried on fishery for the purpose of obtaining roe every autumn since 1945, practically all the spawning fish being caught. The roe has been taken to a fish hatchery and the fry reared in ponds to one summer old fish, which have been partly released down stream. Scale samples have been taken of a small quantity of fish in connection with the fishing in Kallströmmen and some of the trout were marked before being returned to the water.

Although the material is rather incomplete, I have considered it to be worth using to try to show how considerably the regulation interferes with the fish spawning in the streams.

Table 2. The fish species of the investigated lakes.

Lake	Trout	Char	Grayling	Burbot	Whitefish
Rensjön	+	+		+	
Anjan ...	+	+	(+)	+	
Torrön ...	+	+	+	+	
Juveln ...	+	+	+	+	
Kallsjön	+	+	+	+	+

Table 3. Number of years spent in the stream expressed as percentage of total sample.

Lake	Number of years in the stream						Size of sample
	1	2	3	4	5	6	
Rensjön	4.8	25.8	38.7	22.6	8.1		62
Anjan ...	4.5	40.9	30.3	22.8	1.5		66
Torrön ...	10.1	37.3	31.3	18.2	3.1		99
Juveln ...	8.9	42.2	29.6	12.6	5.2	1.5	135
Kallsjön	4.2	29.2	41.6	25.0			24

The Trout Populations

The main spawning-grounds for the trout were the previously mentioned streams between the lakes. In both the two lakes furthest up in the system. Rensjön and Torrön, they consist of the outflowing streams Rensjöån resp. Ängströmmen, while the trout in Anjan, Juveln and Kallsjön make their way to the inflowing streams, namely the lower Rensjöån, Ängströmmen and Kallströmmen. Spawning migration upstream also occurs, however, to a lesser extent in certain small inflowing streams in all the lakes.

Spawning takes place in September and October and, according to observations made in the Rensjöån, hatching occurs at the end of April or the beginning of May. This is also in agreement with the time for the hatching of trout roe in the fish hatchery at Bonäshamn, situated at the outlet from Kallsjön, where the water temperature in the troughs is about the same as in the lake. The yolk-sack has, therefore, probably not been reabsorbed and the fry become ready to swim before the end of May or the beginning of June.

The young fish remain for the first years of their lives in the stream, which leaves its mark on the growth zones of the scales during this time. In table 3 the number of years spent in the stream is shown according to scale readings on the fish caught in the lake in the summer. As may be seen from this, the stay in the rivers lasts from one to five years, most frequently two to three years. This is quite in accordance with direct observations made of migration upstream in the fish ladder at Rensjön, where the majority of trout migrated up to the lake during their second to sixth summer (RUNNSTRÖM 1949).

It is interesting to note that the trout in the Rensjöån migrate up to the lake against the current at the same age stages as they migrate down to the lake with the current, as is, for example, the case in Anjan and Juveln, where spawning only occurs in the inflowing streams. It should be a fruitful task to compare the behaviour of these young fish in the same way that HOAR (1951) compared the different species of salmon on the West Coast of America.

The catches in gill nets from the summer fishing in the lake mainly represent immature fish 3—7 summers old apart from a few older fish, as

Table 4. The age composition of samples of trout from the summer fishery expressed as percentage of total sample.

Lake	Age groups											Size of sample	
	3	4	5	6	7	8	9	10	11	12	13		14
Rensjön	17.1	11.4	31.4	20.0	17.2			2.9					35
Anjan ...	7.6	42.4	30.4	10.6	1.5	3.0	3.0					1.5	66
Torrön	22.2	35.3	21.2	14.1	4.1	2.0	1.0						99
Juveln...	17.8	27.4	27.4	13.3	5.2	5.2	0.7	0.7	0.7		0.7	0.7	135
Kallsjön		33.3	37.5	25.0	4.2								24

Table 5. The age composition of spawning trout expressed as percentage of total sample.

Lake	Age groups									Size of sample
	6	7	8	9	10	11	12	13	14	
Rensjön ...	13.1	13.1		21.7	21.7	17.4	8.6		4.4	23
Kallsjön ...	5.5	11.0		27.8	27.8	16.9	5.5	5.5		18

may be seen in table 4. Most of these have been caught already the same summer that migration to the lake took place or during the following summer.

The fish, which are going to spawn in the autumn, usually make their way to the streams as early as August and can then be caught by sport-fishermen until the closed season from September 1st. The spawning fish in the Rensjöån and Kallströmmen display great similarity regarding age distribution and the trout seems to be ready to spawn for the first time at the age of 6 years, but attains a very great age as is apparent from table 5.

There is, though, a considerable difference in size between the trout from the two streams, which may be seen in table 6. The largest fish of the controlled trout from the Rensjöån was 71 cm long and weighed 5.7 kg and the mean weight for the whole sample was 2.5 kg. The largest trout from the Kallströmmen had a length of 92 cm and a weight of 8.8 kg, while the mean weight for all the trout was 4.5 kg. As is shown in table 7, the Kallsjö trout at a greater age display a better growth than the Rensjö trout. From the information which could be obtained, it seems that the spawning trout in the Kallströmmen — Sundströmmen — Ängströmmen belonged to the same size group and the fishermen thought that they were from the same population, that migrated within this area. During test fishing in Juveln in September 1938 a trout was caught with a length of 90 cm and a weight of 9.9 kg, that had attained the age of 17 years. In the upper and lower Rensjöån, where no fish can migrate upstream from Kallsjön, the spawning trout are smaller in size.

Table 6. Length and weight of spawning trout from the investigated streams.

Length groups cm	36/40	41/45	46/50	51/55	56/60	61/65	66/70	71/75	76/80	81/85	86/90	91/95	96/100
Kallströmmen: number of fish		1	6	3	1	12	17	25	19	19	5	2	1
mean weight kg		0.8	1.2	1.7	2.4	2.8	3.4	4.8	5.1	6.1	6.2	7.7	—
Rensjön: number of fish	13	4	9	9	14	9	9	4					
mean weight kg	0.6	—	—	1.7	2.3	2.8	3.5	4.6					

Table 7. Growth rate of spawning trout from the main streams and of summer-caught trout from the lake.

	1 ₁	1 ₂	1 ₃	1 ₄	1 ₅	1 ₆	1 ₇	1 ₈	1 ₉	1 ₁₀	1 ₁₁	1 ₁₂	1 ₁₃
Rensjön: spawning fish	5.8	12.8	19.0	26.2	34.1	41.4	46.3	53.6	59.3	63.3	67.3	68.8	—
Kallströmmen: spawning fish	4.8	11.6	18.7	25.7	33.6	41.9	48.8	56.0	64.9	69.5	73.2	75.7	77.3
Kallsjön: summer-caught fish	5.1	10.7	16.8	23.3	27.8	33.0	39.0						

Within the system Kallsjön — Juveln — Torrön the large-sized trout only spawned in the above-mentioned main streams and the trout, which spawn in the smaller inflowing streams, are smaller in size with a maximum weight of approximately 1—2 kg. If one considers the growth of the young fish caught in the summer in Kallsjön (table 7), one finds that their growth is much poorer than the spawning trout from Kallströmmen, which indicates that slower-growing populations from the smaller spawning streams are present here. It seems, consequently, as if we have a large-sized trout population restricted for its spawning to the main streams and populations of smaller-sized fish in the minor feeder streams. This is in close agreement with the conditions in Lake Vättern, where according to ARVIDSON (1935) the trout spawning in the outflowing river, Motala ström, constitute a stock of their own only spawning in this river. This form of trout has an average weight varying during different years from 2.7 to 4.5 kg, while the average weight of the trout spawning in the smaller feeder streams always remains under 2 kg.

Marking experiments carried out on the spawning trout in the Kallströmmen also show that it always returns to the same river for spawning. During the years 1945—1949 119 spawning trout were marked in the autumn in Kallströmmen (table 8). 13 of these fish were caught during the summer fishing at different places over the entire Kallsjön, most of them during the following summer, but some during the second or third summer after the year marking took place. At the spawning-ground in the Kallströmmen 34 of the trout were recaptured, when they returned to spawn again. Approximately 28 percent of the spawning fish accordingly spawn at least twice. Whether these had already spawned before marking could not be determined, as the scales do not show any typical spawning marks. All the recaptured marked spawning fish were released again and two of these were recaptured, which spawned for at least the third time, and of these two one was recaptured a third time, which consequently spawned for at least the fourth time. None of the marked trout were recaptured at other spawning-grounds than in Kallströmmen.

Of the 34 trout, that spawned at least twice, two fish spawned during two consecutive years and one has spawned for the second time the third year after the previous spawning. The majority, 31 fish, have however had a year of rest and spawned the second year after the previous spawning. The two trout, which spawned at least three times, have had a year of rest between every spawning, but the one that spawned yet another time then spawned the following year, consequently 5 years after marking. The marking thus shows very clearly that the greater part of the Kallström trout only spawn every other year.

It has previously been considered probable that the trout in the Rensjöån do not spawn every year either (RUNNSTRÖM op.cit). ARVIDSON (op.cit.) has

Table 8. Marking experiment with spawning trout at the stream Kallströmmen.

Year	Sex	Number of fish caught	Number of fish marked	Recoveries on the spawning-grounds after years					Recoveries in the lake in the summer after years				
				1	2	3	4	5	0	1	2	3	
1945 ...	♂♂	18											
		45	18	12		2 ¹	1 ²						
1946 ...	♂♂	24	6										
		31	14	4					1	1	1 ¹		
1947 ...	♂♂	25	10						3				
		59	36	1	5				1	1	1		
1948 ...	♂♂	18	7										
		17	12	4	1				1	1	1		
1949 ...	♂♂	14											
		48	16	1	5				1				
Total	♂♂	99	23		1					3			
		200	96	2	30	1	2	1	1	4	3	2	

¹ Recovered for the second time.

² » » » third » .

also shown by marking experiments that the large trout in Vättern spawned in the Motala ström at intervals of 1—5 years, the majority, 47.6 percent, at intervals of two years. The sea trout in the River Åvaån differ, because the fish, which return to spawn for the second time, usually do so as early as the following year (ALM 1950). It seems, however, to be a common phenomenon for the large-sized forms of trout to have a year of rest between each spawning. On the other hand the small-sized forms of trout, which remain for their entire lives in small streams, spawn every year (ALM 1939). It is, therefore, not farfetched to come to the conclusion that the intervals between spawning are dependent on the size of the fish.

Roe from the Kallström trout was hatched in the fish hatchery at Bonäs-hamn in the spring of 1945 and the fry were then reared in ponds. In the autumn of 1948 57 females with a mean weight of 250 gr. were ready to spawn and they were placed in a special pond. During the following year up to the autumn of 1949 no losses occurred but only three females were ready to spawn. In the autumn of 1950, however, roe was obtained from most of the females. This shows that the Kallström trout reared in ponds become ready to spawn at a lower age and a considerably smaller size than has been observed in a natural state. Nevertheless this trout has retained its original rhythm, as regards intervals between spawning, and produces roe only every other year. This characteristic seems, therefore, to be genetically conditioned.

It is striking how numerically small spawning populations of large trout are in these comparatively big lakes. In the Kallströmmen it is a matter of 60 fish on an average per spawning season, the females being in the

majority (table 8). In the Rensjöån, where the spawning population could be completely controlled, about 20 fish spawned per season. Taking the marking experiments in the Kallströmmen as a basis, the annual mortality in the spawning population can be estimated at 45 %. On account of the great age of the spawning fish, a very small proportion of the population must attain the age for spawning. It must, in this respect, also be very detrimental for the population that spawning only occurs every other year, as the number of fish which can spawn several times is greatly reduced by the high rate of mortality.

The Water Flow in the Streams after Regulation

On account of the water being stored in the lake during the summer and the damgates being opened in the winter, the natural water flow in the draining rivers is altered in a very far-reaching way, as is apparent from fig. 2, which shows the regulated average water flow in the Kallströmmen during the period 1940—1951 as well as the estimated natural water flow during the same period (broken lines). After the regulation the strong floods during the spring and summer disappear and only inconsiderable quantities of water flow during that time. In the winter, however, the water flow is considerably greater than under natural conditions. The regulation consequently entails a complete reversal of the natural conditions. During wet years quite a steady tapping occurs during the whole spring and summer, but most years the damgates are entirely closed during certain periods in order to save water and the draining river is then laid completely dry below the dam. Table 9 shows the number of days in every month when the water flow in the Kallströmmen was 0 m³/s. With the exception of the years 1943 and 1949, the water during the remaining years was shut off during long continuous periods. During the first year of regulation this took place in

Table 9. Number of days with no waterflow in the stream Kallströmmen.

Year	Month								
	IV	V	VI	VII	VIII	IX	X	XI	XII
1940.....				5		22	22	28	16
1941.....		26	26	16	4	5	5	17	
1942.....	12	31	30	23	29	2	5		
1943.....				3					
1944.....	5	31	27	6			1		
1945.....		9	12	6	6				
1946.....	12	31	16						
1947.....	3	31	30	24	1				
1948.....	21	31	29	27	14				
1949.....		8							
1950.....	5	31	14						
1951.....		28	24						

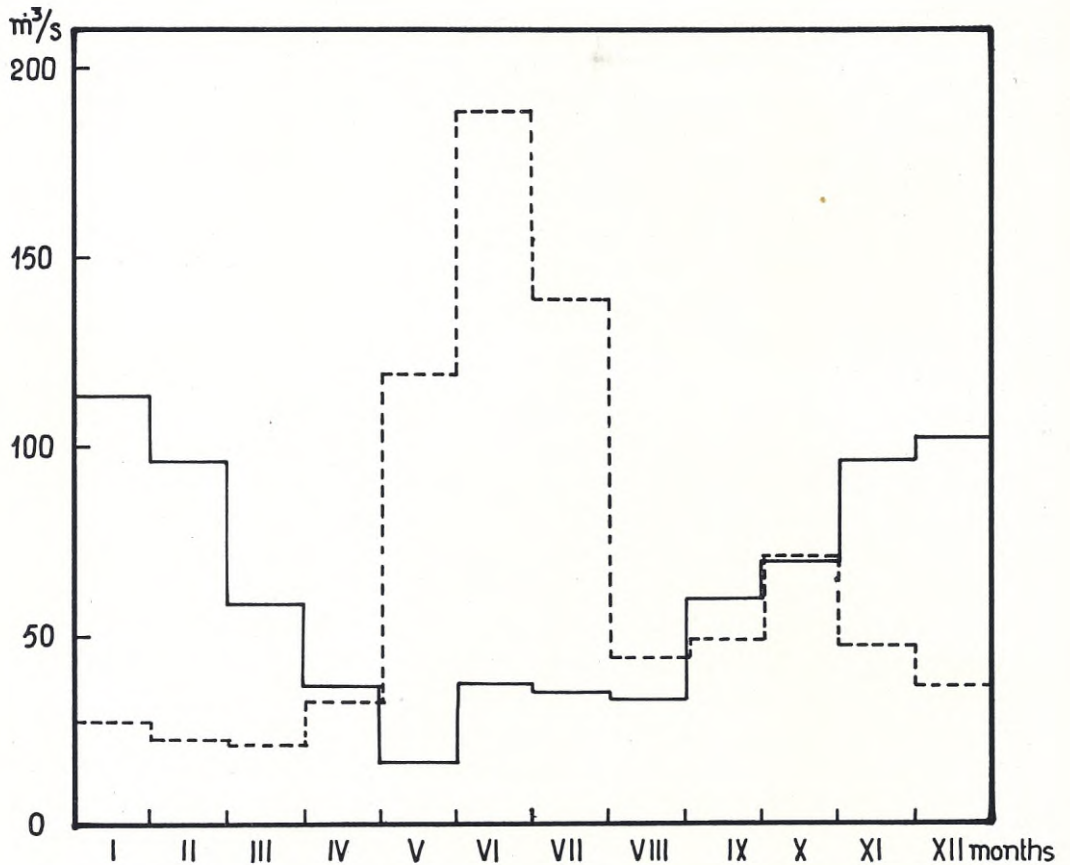


Fig. 2. The regulated average water flow in the stream Kallströmmen during the period 1940—1951 and the estimated natural water flow during the same period (broken lines).

the autumn, which was probably on account of the construction of the lowering canal below the dam. Otherwise the draining has chiefly occurred during May, June and July, during certain years as early as April.

Similar conditions to those in Kallströmmen have also prevailed in the streams Ängströmmen and Sundströmmen. In the Rensjöån the stream was laid dry in the spring and summer during the years 1940—1942 and during the year 1943 as well there was a very negligible flow of water during the period June—September. From and including 1944, however, a certain minimum quantity of water has always been allowed through the entire year in connection with the construction of a fish ladder.

On account of the damming up of the lakes, the lower parts of the feeder streams become flooded and lose their original character of streams in the summer. This is also the case with the smaller feeder streams.

The Effect of the Regulation on the Trout Population

As is evident from the above account of the water flow, at least as great quantities of water are run into the regulated rivers during the trout's spawning season in September and October as under natural conditions and the fish are not prevented from spawning here. On account of the laying dry in the spring the roe or the newly hatched fry is destroyed, however, during most years. The natural nursery grounds for the young fish also disappear, owing to the streambeds lying dry in the summer.

The dam itself also constitutes a hindrance to migration for the fish. This is particularly disastrous in the lakes, where the trout migrates down the outflowing river for spawning, so that there is no possibility for it to make its way up to the lake again, which gradually reduces the population. These conditions apply to the main streams between the lakes. In the smaller feeder streams the water flow remains unchanged, but on account of the raising of the water level in the lakes in the summer and autumn the lower parts of the streams become flooded and the spawning-grounds are to a greater or lesser extent reduced in this way. It is, however, first and foremost the large trout's spawning-grounds in the main streams, that are the most affected by the regulation.

If we look at the different lakes, the large trout in Torrön has had its only spawning-ground in the outflowing river, Ängströmmen, destroyed and owing to there being no fish ladder the old population has disappeared. Before the regulation there was profitable fishery with gill nets here at the time the large trout migrated down to the spawning-ground, but this fishing is now a thing of the past. As to the feeder streams, the spawning-grounds in the Hobergsån are entirely destroyed on account of overdamming, but on the other hand another stream, Gånälven, which was previously closed to trout owing to a waterfall, is now accessible.

In Rensjön, where the trout chiefly spawn in the upper part of the outflowing stream, Rensjöån, the spawning-grounds were laid dry during the years 1940—1943 and these years have probably not contributed at all to the trout population in the lake. From the year 1944, however, a certain minimum quantity of running water has been allowed in connection with a fish ladder being constructed beside the dam. Control of this ladder has shown that both the spawning fish as well as the young fish growing up in the stream have had a chance to migrate up to the lake (RUNNSTRÖM 1949).

In the lower part of the Rensjöån, where the trout from Anjan has its main spawning-ground in a stretch from the mouth up to a waterfall preventing further passage upstream, no laying dry has taken place, partly on account of the abovementioned tapping from Rensjön, partly on account of feeder streams further down the river. The spawning area has been greatly reduced

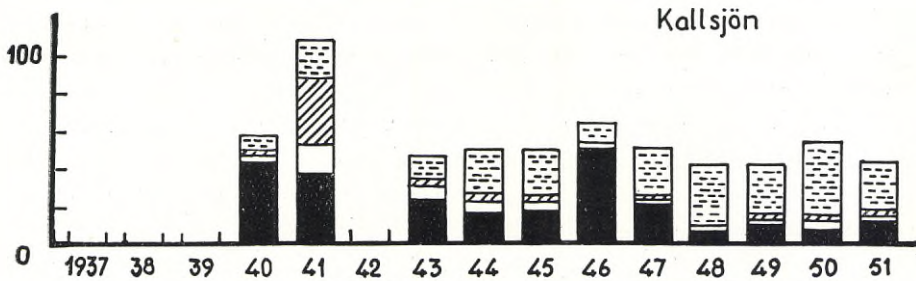
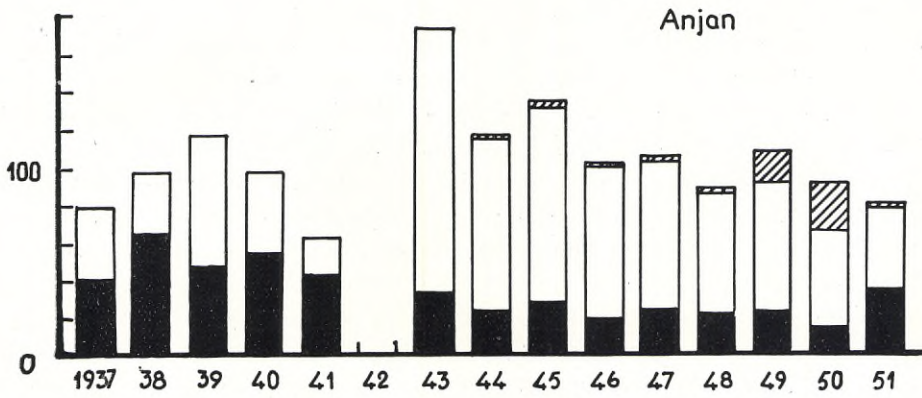
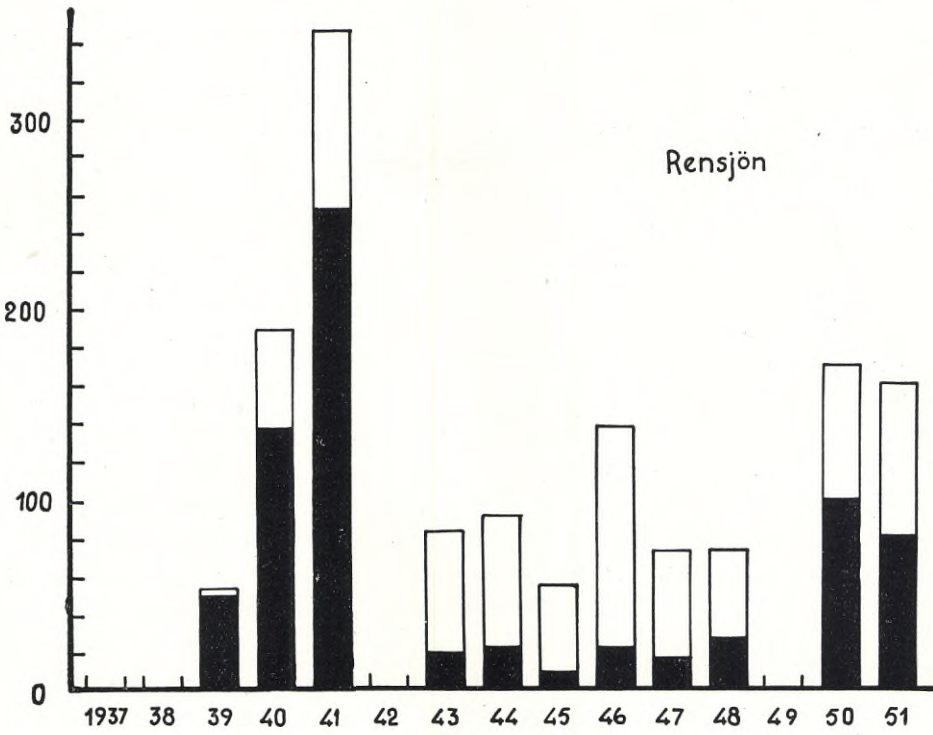
here, though, owing to the damming of the lake. This is also the case for the spawning-grounds in the smaller streams.

In Juveln the previous main spawning-grounds in the Ängströmmen have entirely disappeared on account of the water being retained in Torrön. Even in the years when a certain tapping takes place during the spring and summer, the spawning area has been greatly reduced by the damming up of Juveln. Only spawning-grounds in the smaller streams remain in this lake as well as the Ycklan, a short stream with plenty of water, which constitutes the outflow for Lake Äcklingen into Juveln.

In Kallströmmen, which is clearly the large trout's only spawning-ground in Kallsjön, it may be seen from table 9 that the water is shut off most years for the greater part of the spring and summer. The bottom below the lowering canal, however, forms quite a large-sized basin, where water is left so that this area never becomes entirely dry. It is, therefore, possible for the roe and the fry to survive here, especially if water is allowed to run through at not too short intervals. The fact that spawning occurs in this basin is apparent from trout roe being found in the stomach of other fish caught here. Fry have also been observed in the autumn. From and including the year 1945 the greater part of the spawning population has been caught every autumn for obtaining roe. This can be done very effectively by shutting the damgates and lowering the water level in the basin below, so that the fish are trapped. No tendency towards a reduction of the spawning population in the Kallströmmen can as yet be observed from the fishing results, as is apparent in table 8. This is also the case for the years 1950 and 1951 when 60 resp. 53 spawning fish were captured. According to the age composition of the spawning trout (table 5) the first year class influenced by the regulation, namely year class 1941, probably was part of the spawning population as early as the autumn of 1946 and since then the number of year classes influenced has increased successively and in the years 1950 and 1951 the spawning population should have consisted for the greater part of the year classes 1941—1945, all of which arose after the regulation. In spite of this no decrease in the numbers of the spawning population can be observed. As only the year classes 1944 and 1945 obtained a reinforcement through a small release of one summer old trout below the Kallströmmen, it must be presumed that the recruitment for the greater part has occurred on the basis of natural spawning in the Kallströmmen during the first years regulation took place, which must depend on the previously mentioned

Fig. 3. Number of fish per 100 net-men caught at the summer test fishing during the period 1937—1951.


 trout, char, grayling, whitefish.



circumstance that the stream was not laid completely dry by the closing of the damgates.

Of the remaining spawning streams in Kallsjön, where the population consisted of a more stunted form of trout, the biggest, Sundströmmen, has entirely disappeared as a spawning-ground partly on account of being laid dry and partly through a larger area being flooded, while the other streams have only been affected by the regulation to a lesser extent.

The damage, that has been done to the trout's spawning-grounds on account of the regulation, is of such an extent that it can be taken for granted that the recruitment of the trout population of the lakes has been considerably reduced, which should react on the fishing results. As may be seen from the foregoing paragraphs, there has been no control on the populations of spawning trout in the different rivers or streams with the exception of the upper Rensjöån and the Kallströmmen. The investigation must, therefore, be chiefly based on the results of the gill net-fishing in the summer. The population, which forms the basis for the summer fishing, is recruited from all the spawning streams and it is not possible, taking this as a basis, to analyse how the regulation affected the various spawning-streams or to separate the offspring of the large trout from the smaller forms of trout. The summer fishing is also dependent on many factors, such as weather and wind and the movements of the fish, and the yield does not express the size of the population as well as fishing during the spawning season. As the test fishing covers quite a long period of time, however, one could expect to be able to see from it if there is any decided tendency in the development of the fishery since the regulation.

In figg. 3 and 4 are given the catches for the test fishing with gill nets, which has been carried out in the different lakes during the years 1937—1951, the bars showing the number of fish of different kinds obtained per 100 netmen. The relation between the different kinds of fish has been marked in every bar, the number of salmon trout being indicated in black at the foot of the bar.

If one first considers the total catch of all the kinds of fish, one finds a general tendency towards a decided increase in the catch the first year after the damming up. In Lake Torrön the first large damming up occurred in the year 1938 and the damming was increased still further in the year 1940. There were great catches from the summer fishing during these years. In the other lakes the first damming took place in the spring of 1941 and here, too, an increase in the catch is to be found with the exception of Lake Anjan, where the earth-layer in the overdammed area was very thin and was quickly eroded away. As has already been discussed in my paper on the char (RUNNSTRÖM 1951), the fish made their way to a great extent to the overdammed areas, where plentiful food supplies were available, so that very good catches could be obtained with gill nets, which are mainly

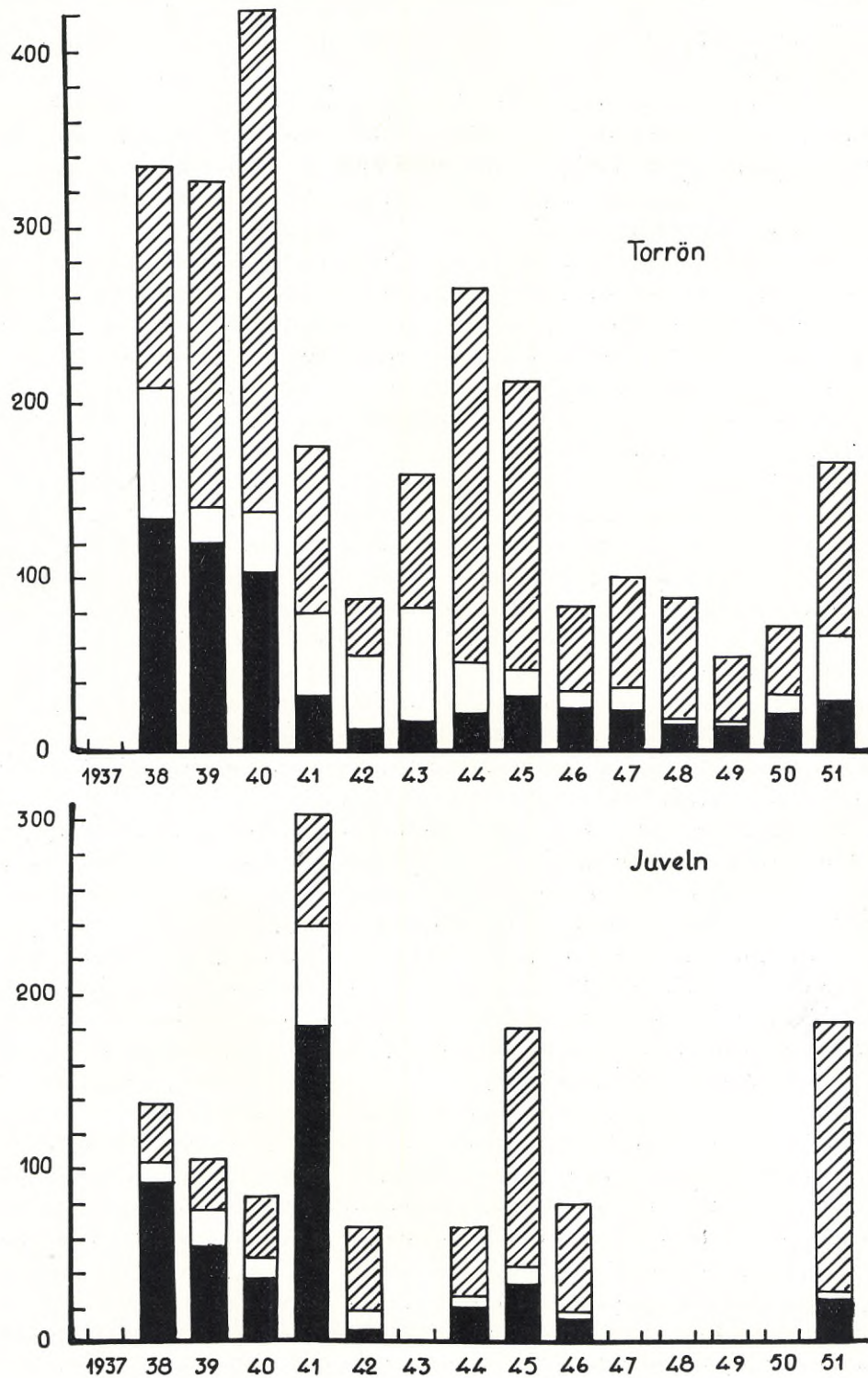


Fig. 4. Explanation, see fig. 3.

laid out from the shore in shallow water during the summer fishing. After the loose earth-layer had been eroded away, which occurred during the first years after regulation on the more exposed shores, the overdammed areas partly became rather sterile stone bottoms, where no rich algal vegetation has time to grow during the dammed up period in the summer, and the large shoals of fish in the litoral area was only of a temporary nature.

After the temporary increase in the fishing during the first year after damming, the catches have varied very much from year to year, which is often the case with the summer fishing, and it is difficult to draw any definite conclusion as to whether a reduction has really occurred in the total catch as compared to the catch before the regulation. In Anjan, from which lake we have the most complete series both from the time before and after the regulation, one does not find any apparent tendency towards a reduction in the catch the years after the regulation took place. As I have already discussed in another paper (opus cit.) the regulation does not seem to have caused any decrease in the recruitment of the population of char although rather a great deal of the roe is laid dry and destroyed by the lowering of the water level on the spawning-grounds in the lake in the winter. This is probably also the case with the whitefish in Kallsjön. As far as the grayling is concerned, it spawns in the spring in the lake, when the water level is rising, so that there is no reason to suppose that the roe is damaged in any way. If any reduction should have occurred in the catch from these kinds of fish, it probably more likely depends on the fish making their way to a lesser extent to the new sterile bottoms rather than to a reduction in the numerical strength of the population.

Even if no tendency can, accordingly, be found towards a reduction in the total catch, the catch diagram seems to show a rather decided decline as far as the trout is concerned. This can, perhaps, be seen still more clearly in table 10, which shows the percentage of trout in the catch during the different years. From having been dominant in the catches, the percentage of trout after the regulation has been considerably reduced in relation to the other kinds of fish. This is the case for all the lakes with the exception of Rensjön, where the trout fishery shows a decided tendency towards recovery during the years 1950 and 1951 (*vide iufra*).

Judging by these results, it should be possible to draw the conclusion that the consequences of the regulation on the spawning-grounds affect the trout spawning in the streams to a greater extent than the other kinds of fish spawning in the lake, such as char, whitefish and grayling, and that an appreciable reduction in the trout population has occurred in relation to the other populations of fish.

Admittedly a certain amount of damage is done on the spawning-grounds to the species of fish spawning in the lake in the autumn and the roe is decimated in the spring by the lowering of the water level. There is, however,

Table 10. The catch of trout during the summer fishery expressed as percentage of total catch.

Year	Torrön	Juveln	Rensjön	Anjan	Kallsjön
1937				52.0	
1938	40.4	67.0		66.0	
1939	37.2	52.5	94.6	41.0	
1940	24.4	44.2	72.8	58.0	79.5
1941	17.7	60.0	73.4	67.0	35.8
1942	14.6	11.1	—	30.0	
1943	11.0	—	24.1	19.0	50.0
1944	8.1	30.6	24.3	20.0	34.0
1945	15.3	18.7	17.6	21.7	36.8
1946	29.4	18.5	15.6	20.4	81.1
1947	22.0		22.9	23.4	43.5
1948	15.5		38.6	25.0	19.0
1949	24.0			21.0	27.7
1950	30.4		59.2	18.2	17.4
1951	17.8	13.9	50.5	44.5	29.7

no limitation of the areas where the fry grows up during the summer and the fry probably has better chances of survival through decreased intra-specific competition. As far as the trout is concerned, not only is the roe reduced in the spring but still more important the places, where the fry grows up in the streams are destroyed. The recruitment certainly is too small to keep the population at the same size as before the regulation.

Management of Regulated Lakes

In order to compensate for the damage on the spawning-grounds and to improve the recruitment of the trout population, the regulating association has primarily made releases of fry. The first few years fry of trout were planted but later on nothing but fingerlings were used. The number of fry and fingerlings planted may be seen in table 11. The fingerlings have been released in the streams, as far as was possible, but the majority had to be put in the lake. It has not been possible to prevent the previously mentioned appreciable reduction of the trout population, in spite of these extensive releases, and in the formerly good trout waters, char, grayling and in Kallsjön whitefish now dominate.

Some experiments have been made by the Institute with the marking of trout fingerlings by fin-cutting, in order to control their effect on the population (table 12). The experiments have been carried out partly in Rensjön and the upper Rensjöån, partly in another regulated lake, Storsjouten, which has been regulated in the same way as the lakes dealt with here, the main spawning-ground in the outflowing river being totally destroyed.

Table 11. Number of fry and fingerlings planted.

Lake	Fry		Fingerlings	
	Year	Number	Year	Number
Rensjön			1943—51	57,000
Anjan	1941	20,000	1943—51	54,000
Torrön	1940—45	171,000	1943—51	66,800
Juveln	1941, 1945	13,500	1943—51	50,850
Kallsjön	1941—46	744,700	1944—51	355,000

In Rensjön, where the fingerlings were released direct in the lake, no recaptures were made during the test fishing in the years 1948—1951. Of those released in the year 1948 in the Rensjöån only 3 of the fingerlings were recaptured in the year 1951 in the fish ladder, where migration upstream is controlled every year. The control for 1952 has not yet been concluded. In Storsjouten the fingerlings were planted in a small feeder stream, where the trout go up to spawn. Of the fingerlings marked in 1948 39, or 0.38 percent of the fish released, were recaptured during the summers 1950—1952. During these years 1,025 trout of the same length group were caught, so the marked trout only constituted 3.8 percent of the population, which arose on the basis of natural spawning. Only 4 of the trout marked in 1949, which were of Danish origin, have been recaptured during the summers 1951—1952.

What can be the reason for the poor results from these releases? When the fingerlings are planted direct in the lake, as in Rensjön, they have had to compete with the char. An experiment, made by SVÄRDSON (1949), concerning the competition between trout and char when rearing fry from these two species and their hybrids to fingerlings, showed that the char has far better powers of survival than the trout. The trout, which under natural conditions grows up in the streams, is not subjected during its first years to competition from the char, but for the fingerlings, which are planted direct in the lake, this competition is obviously overwhelming. In the experiments, where the fingerlings were planted in spawning streams, the streams have been occupied in advance by trout fingerlings, which already filled the territory and the strong intra specific competition probably explains the small number of survivors.

As there are hardly any streams to be found with a sufficient water flow that have not already got a natural trout population in these lakes, the releases seem to be rather hopeless unless a change is made to rearing them to a size corresponding to the size of the trout when ready to migrate to the lake, which would probably be a less financially profitable undertaking.

Another way to compensate for the damage to a certain extent is to allow a certain minimum quantity of water to pass into the stream and to install

Table 12. Marking experiments with fin-cut fingerlings of trout reared in ponds

Locality of planting	Year	Fin-cut	Number of fish marked	Recoveries					
				1948	1949	1950	1951	1952	Total
Rensjön	1947	r. pelvic	3,305						
		l. »	3,839 ¹						
The stream Rensjöån	1948	l. pelvic + fat fin	1,000			3			3
	1949	fat fin	2,300						
Storsjouten	1948	r. pelvic	10,500			13	12	14	39
	1949	l. pelvic	10,500 ¹				3	1	4

¹ Roe imported from Denmark.

a fish ladder in the dams, where the trout goes down in the outflowing stream for spawning. In this way total damage to the places where the fish grow up can, at least, be avoided. As has been previously mentioned, such measures have only been taken in the upper Rensjöån within the group of lakes dealt with here. On account of the low height of the dam and the inconsiderable water flow, which have been necessary here, these measures could be taken without too great costs as compared with the other streams. When this ladder was first built in the year 1944, however, the year classes 1940—1943 of the trout population were destroyed. The first year class, which arose after the regulation, is consequently the year class 1944 and as the summer fishing in the lake is based on 3—7 summers old fish, it can be expected that fishery from a recovered population can first be carried on in the summer of 1950. It is also apparent from fig. 3 as well as table 10, that the catches of trout during the years 1949 and 1951 showed a marked increase in Lake Rensjön.

It appears, thus, that the building of fish ladders combined with a certain water flow seems to be the only measure as yet taken, which to a certain degree can compensate for the effect of the regulation on the trout population. Unfortunately these measures entail such great costs, particularly as regards the necessary water flow, that they usually far exceed the value of the fishing and the Water Court has, therefore, in many cases been unable to impose such liabilities. Only an amendment of the Water Laws with an injunction about a certain water flow in the rivers should be able to bring about an improvement in these conditions.

Summary

A great number of lakes in the North Swedish rivers are regulated by means of dams for the purpose of obtaining water power, the water being stored in the lakes during the summer and autumn to be tapped out later on during

the winter. During the season, when damming up occurs, the outflowing rivers are laid dry most years for long periods, affecting the spawning-grounds and places where the trout grows up. Test fishing has been carried out in five regulated lakes in the River Indalsälven during the summers 1937—1951 in order to investigate the effect of the regulation on the trout population. This has shown that the catch of trout has decreased since the regulation both in total size as well as in relation to the other kinds of fish in the lakes. Extensive releases of trout fry and fingerlings have not been able to compensate for the damage done to the population and experiments with fin-cut trout fingerlings have shown that these releases are of very little use, probably on account of intra- and interspecific competition. The only way to eliminate the damage in part seems to be that a certain minimum water flow should always be allowed in the streams and that fish ladders are constructed at the dams in those cases, where the salmon trout goes down the outflowing river to spawn.

References

- ALM, G., 1939. Investigation on growth etc. by different forms of Trout. *Rept. Inst. Freshwater Res. Drottningholm*, 15: 1—93.
- 1950. The sea-trout population in the Åva stream. *Rept. Inst. Freshwater Res. Drottningholm*, 31: 26—56.
- ARVIDSSON, G., 1935. Märkning av laxöring i Vättern. *Rept. Inst. Freshwater Res. Drottningholm*, 4: 1—16.
- HOAR, W. S., 1951. The behaviour of Chum, Pink and Coho salmon in relation to their seaward migration. *Journ. Fish. Res. Board. Canada* 8 (4): 241—263.
- RUNNSTRÖM, S., 1949. Control of trout migration by a fish ladder. *Rept. Inst. Freshwater Res. Drottningholm*, 29: 85—88.
- 1951. The population of char, *Salmo alpinus*, LINNÉ, in a regulated lake. *Rept. Inst. Freshwater Res. Drottningholm*, 32: 66—78.
- SVÄRDSON, G., 1949. Competition between trout and char (*Salmo trutta* and *S. alpinus*). *Rept. Inst. Freshwater Res. Drottningholm*, 29: 108—111.

Spawning Behaviour of *Leuciscus rutilus* (LINNÉ)

By GUNNAR SVÄRDSON

During the very last days of May or at the beginning of June, the roach, *Leuciscus rutilus* (L.) gather at the shore close to the buildings of the Institute of Freshwater Research. The fish accumulate for some while in the shallow water and actual spawning is performed on sunny days when the water temperature, close to the shore, is 17° Centigrade or higher. The spawning lasts 2—3 days and after that the fish suddenly leave the shallowest water and disappear. There is a striking difference between one day where many thousands of fish move about in the water, splashing and shaking the steams of the reeds, and the next day when not a single fish is visible.

Good opportunities for study are sometimes given, especially when the roach spawn under the landingstage of the Institute. The fish are not shy and can sometimes be observed for hours within a range of roughly one metre. The following short report is based on scattered observations made during several years.

Spawning ground

The roach spawn along the shore in the innermost water belt. The spawning ground may thus have a breadth of only one or two metres but a length of hundreds of metres. Water depth is usually less than 15 centimetres and the fish may move so close to the shore that their dorsal fins are seen above the water level.

The vegetation on the spawning ground is principally common reed (*Phragmites communis*), *Carex* species and the submerged *Myriophyllum*. As will be shown later (*vide infra*) concentrated tufts of vegetation are of special significance for the release of actual pairing.

Spawning behaviour

A most striking fact in the spawning behaviour of the roach is the different distribution of the sexes. The spawning ground is covered by the males, which patrol the shallowest water in large numbers. They have no territories



Fig. 1. Dispersal of the males on the spawning ground (left) and their pursuit of an intruding female, which rushes towards the densest vegetation (right).

but are concentrated so there are 20—50 specimens on every square metre of the spawning ground. The males move about constantly in irregular circles. Individuals, identifiable by their size, loss of a few scales or some other slight injury can for a short period (say 15 minutes) be seen over and over again within the same square metre, but when they are followed more carefully it is found that they spread with time. Especially after a rush (*vide infra*) they do not return to their former place. Displacement up to 3—4 metres has been observed during half an hour. The roach's behaviour in this case is significantly different from that of the bream (*Abramis brama*).

There is some nipping amongst the males but no serious aggressive display. If a male chases another male for a few decimetres a »follow-up»-reaction is prompted in the nearby males. Three or four males may thus take part in a short rush. Almost certainly this chasing is due to a mistake, the fleeing male being mistaken for a female.

Females now and then enter the »male belt» from the outside, i.e. the deeper waters. They are immediately chased by the males and the rush in this case is more rapid and longer, more males participating than when a male happens to be the »leader». If the female turns out again, which probably is the case when she is not ready to spawn, the pursuit is discontinued and the males return to the inner belt. But in other cases the female rushes to the nearest tuft of dense vegetation, where one or more males adhere to her laterally and a batch of eggs is spawned and fertilized. Trembling movements can sometimes be observed accompanying the actual pairing but the performance is short and very difficult to observe carefully due to the water movements and the splashing. The eggs stick to the vegetation or the obstacle which stopped the rush of the party. A small piece

of wire netting had once fallen into the water and it was observed that spawning took place when the female could not escape through the netting. Spawning was also released on the outside of a trap and eggs were found. This indicates that when the advance of the female is impeded and the male or males gain contact with their pearl organs on the sides of the body, egg-laying is released. The chasing most probably serves as a general stimulus but the stimuli for egg-laying seem to be the obstacle preventing further movement and the contact with the male's pearl organ.

Reaction of trapped roach

In order to check the different distribution of the sexes on the spawning ground, as judged by observation, a simple funnel trap was placed in the »male belt» on June 3, 1951. In few hours it was entered by 42 fish. All but three were males and the observational results thus verified. Age and total length were:

	3	4	5	6	7 years
males					
numbers	3	16	15	4	1
total length, mm . . .	105	131	145	167	184
females					
numbers	—	—	3	—	—
total length, mm . . .	—	—	166	—	—

When the fish had entered the trap and penetrated the wire-netting for a while without being able to join the fish moving outside, a special reaction was released. They withdrew a few centimetres from the netting and leapt into the air. The jump could reach at least 15 centimetres above the water level. It was very interesting to see how the first two roach captured leapt in the air over and over again though among the hundreds of fish moving outside the trap only an occasional fish leapt when a party of spawning fish was splashing in the densest vegetation. The reaction »leaping in the air» was thus released in the roach when an obstacle had repeatedly hindered their swimming straight forward.

Sometimes after roach spawning, dead fish have been found on floating bundles of dead stems of *Phragmites*. Living fish too have been suddenly seen to frisk about on such bundles of reeds for a few seconds until they happen to fall back into the water. The reaction of the trapped fish suggests that this »airdance» has nothing to do with normal spawning behaviour but might be accidentally released when the spawning fish are hindered by too thick vegetation. Probably it is an escape reaction.

Discussion

The spawning activities of *Leuciscus erythrophthalmus* (L) and *Abramis brama* (L.) were previously described (SVÄRDSON 1949). Further information about the size of the bream territories was given by FABRICIUS (1951).

The report on *Leuciscus erythrophthalmus* failed to point out that in this species as well the distribution of the sexes on the spawning ground differs strikingly. This species has, in fact, a »male belt» where the individuals do not hold territories. In the bream, however, this male belt is broken up into the territories of the males. This gives a much lesser concentration of the males.

Apart from the bream's holding territories and a tendency for diving performances when a male pursues an intruding female (this is in accordance with the localization of the pearl-organs which in the bream are concentrated on the head and forward part of the dorsal), the spawning behaviour of the three species is similar. There are more species within each genus but their spawning has not been studied as yet and it is not known if territory-holding is an inherent trait of the genus *Abramis* in contrast to the genus *Leuciscus*.

Hybrids *Leuciscus erythrophthalmus* × *L. rutilus* are recorded and were described by JÄCKEL in 1864 as a different species, *Scardiniopsis anceps* (LILLJEBORG 1891). They are intermediate in most characters. The occurrence of hybrids is not surprising when the spawning behaviour of the two species is similar and both seem to miss important specific social releasers (cf. TINBERGEN 1951). The hybrids, however, seem to be rare and this may mainly be due to the fact that there are differences as a rule in their spawning periods, *L. erythrophthalmus* being the latest spawner.

It is more important that the intergeneric hybrid *Abramis brama* × *Leuciscus rutilus* is also found in nature. It was described by BLOCH in 1784 as the new species *Cyprinus Buggenhagii* and its hybrid nature was first recognized by GÜNTHER in 1868 (LILLJEBORG 1891). In this case the different spawning habits are obviously overcome. Information about their frequency is scanty. LILLJEBORG knew of 11 records from Sweden but LÖNNBERG (1915) states that these hybrids are fairly common. It is not known whether they have the accelerated growth that is typical for hybrids within *Salmo* (SVÄRDSON 1944) and sunfishes (HUBBS and HUBBS 1931). A closer investigation on their occurrence, sterility and growth would be of great interest.

The unbalanced sex-ratio of the trapped sample of spawning roach indicates how such ratios can be obtained in spawning fishing in other species as well. In perch, whitefish and char there must be a concentration of the males on the spawning ground as in roach, for fishing during the spawning season gives a preponderance of males in these species. This in turn probably means that there is a »female belt» outside that of the males, surrounding

the spawning sites. Apart from the spawning period the sexes in all the discussed species tend to occur in roughly equal numbers.

Finally it may be pointed out that shyness is greatly reduced in all the studied cyprinid species when they spawn. This agrees with the statement made by TINBERGEN (1951) that instinctive performances tend to raise the threshold for the release of other instinctive reactions.

References

- FABRICIUS, E. 1951. The topography of the spawning bottom as a factor influencing the size of the territory in some species of fish! *Rept. Inst. Freshwater Res. Drottningholm* 32: 43—49.
- HUBBS, C. L. and LAURA HUBBS. 1931. Increased growth in hybrid sunfishes. *Papers Mich. Acad. Sci. Art and Letters*. 13: 291—301.
- LILLJEBORG, W. 1891. Sveriges och Norges fiskar. Part III. Uppsala.
- LÖNNBERG, E. 1915. Sveriges ryggradsdjur. III. Kräddjur, groddjur, fiskar. Stockholm.
- SVÄRDSON, G. 1944. Arv och miljö. *Lantbruksveckan 1944*: 325—338. Stockholm.
- 1949. Note on spawning habits of *Leuciscus erythrophthalmus* (L.), *Abramis brama* (L.) and *Esox lucius* L. *Rept. Inst. Freshwater Res. Drottningholm*, 29: 102—107.
- TINBERGEN, N. 1951. The study of instinct. Oxford.

The Coregonid Problem. IV. The Significance of Scales and Gillrakers

By GUNNAR SVÄRDSON

Contents

I. Material and Methods	204
II. Results	205
The Correlation Between Body Length and Number of Scales and Gillrakers	205
Transplantations	210
Evidence from Selection Experiments	220
Evidence from Hybrids	223
III. Discussion	225
Scales	225
Gillrakers	228
Ranking of Populations	229
IV. Summary	230
V. References	231

I. Material and Methods

A considerable number of samples of whitefish have been collected from lakes spread over the entire country as well as from the Baltic, in order to shed light on the question as to the taxonomy and distribution of the whitefish in Sweden. Practically all the samples have consisted of fish, which were caught during the spawning season. This is of great importance, as has previously been pointed out (SVÄRDSON 1949, 1951), as it is otherwise extra difficult to distinguish between specimens belonging to different species which happen to have been caught at the same time. Even with spawning fishing it does not seldom happen that a sample is heterogenous and considerably complicates the elucidation of the characteristics of different populations.

The samples obtained were preserved in formalin after scales for age analysis had been taken from all the specimens and their total length recorded. In certain cases the preserved samples were later transferred to 70 per cent alcohol, but in the greater number of cases they have been permitted to remain in the formalin until a biometric investigation could be made.

Especial importance has been given to utilizing the transplantations of whitefish from one water to another, which have been undertaken for purely practical purposes. Such transplantations are usual in Sweden, but in the majority of cases they cannot be used as experiments regarding taxonomic constancy, as the water, to which the transplantation is made, must preferably be free from whitefish. In addition the material transplanted must be identified with certainty. Finally one must be tolerably sure that no further transplantations have been made before or after the one to be studied.

A great number of people have been instrumental in the collecting of material and the often time-consuming investigations, which have been necessary to determine whether a transplantation of whitefish fulfills the demands just mentioned. The following Fishery Assistants have kindly contributed in different ways to the collection of the extensive material for examination: N. I. ADOLFSSON, Motala, E. HALVARSSON, Kälarne, A. ANDERSSON, Norrtälje, A. LURÉN, Nyköping, M. TIDEMAN, Linköping, G. LÜNING, Eksjö, B. JOHANSSON, Växjö, U. LUNDIN, Västervik, G. CHRISTIERNSSON, Kalmar, G. IVARSSON, Visby, G. ISAKSON, Osby, J. WIDERBERG, Sjöholmen, J. E. JOHANSSON, Trollhättan, E. A. SKOGLUND, Borås, F. OLOFSSON, Mariestad, P. HJORT, Mariestad, L. STENBERG, Karlstad, H. WIDERBERG, Köping, H. FORSLIN, Gävle, M. OLSSON, Sundsvall, R. STARK, Ålandsbro, B. LUNDGREN, Östersund, H. PETERSON, Sundsvall, R. GYDEMO, Bergsholmen and E. MATTSON, Luleå. The author would like to express his sincere thanks to all these gentlemen.

In addition the staff of the Institute of Freshwater Research have helped to collect samples of whitefish during the journeys, which they have made to lakes that are regulated for the purpose of obtaining greater quantities of water-power. The monotonous and tedious task of biometric examination has been carried out by Fishery Assistant GÖSTA MOLIN and later, for the most part, by Mr. NILS OLOF ÖSTERBERG. The author would also like to express his gratitude to the Natural Science Research Council of Sweden for financial support contributed to the investigations.

Up to the spring of 1952 totally more than five thousand specimens of whitefish have been examined and at the same time approximately two thousand additional specimens were preserved, which have not yet been studied.

II. Results

The Correlation Between Body Length and Number of Scales and Gillrakers

In an earlier paper (SVÄRDSON 1951) it was presumed that a positive correlation existed between average body size in a whitefish population and the number of scales, which this population had along the lateral line. In order to investigate this correlation more closely a comparison was made of all

the whitefish populations hitherto examined that are spontaneous, that is to say those regarding which it is not known that man has contributed to their present distribution (Table 1). The table contains particulars concerning the average standard length (not total length) of the spawning specimens of the population in question, particulars of the average number of gillrakers and scales as well as the number of specimens examined with regard to the respective characters. It should be particularly emphasized in this connection that the number of scales in the lateral line is defined so that the scales on the tail are included as well. This means that the figures in the table, as was the case in previous papers in this series, are a few units higher than the figures obtained if one only counts the scales on the body itself. The modification of the definition, as compared to a stricter application, has arisen for practical reasons, as it is easier to count all the scales than to decide where one shall stop counting at the beginning of the caudal fin.

The 94 spontaneous whitefish populations thus far biometrically examined are of extremely varying size. Completely dwarf-sized forms are found which when spawning, at 2—3 years of age, have not attained a greater standard length than 79 mm, that is to say less than the length of one summer old fish in populations with better growth. The largest populations yet found attain a standard length of 440 mm. All sizes between these extremes are represented. The number of scales along the side of the body varies between an average of 76.5 and an average of 101.4, while the individual variations are naturally still greater.

Even a cursory glance at table 1 shows that on the whole the number of scales increases regularly from the undersized populations up to those with an approximate average length of 350 mm. After that the correlation is less marked. A statistic examination has shown that body length and number of scales display a correlation coefficient of 0.7040, which in all probability (P. much less than 0.001) is real. The supposition previously expressed has thus proved to be correct and we find that *the number of scales along the side of the body increases with the body size of the population.*

The number of gillrakers on the other hand shows a tendency to decrease as the populations in table 1 become increasingly large in size. This inversed correlation is likewise statistically certain and the coefficient amounts to — 0.4297 (P less than 0.001). We can thus establish that *whitefish populations with few gillrakers display on an average a better growth than populations with numerous gillrakers.* This also agrees with what has been generally observed in that area in Europe, in which the variations of the whitefish have been more closely studied. The fact that there are decided exceptions — in both directions — cannot change the general rule.

As there is reason to consider populations with about the same number of gillrakers as related and often belonging to one and the same species (*vide infra*), three groups of populations probably constituting three different

Table 1. Average numbers of gillrakers on the first left arch and average number of scales along the side of the body in 94 different Swedish whitefish populations, grouped according to average standard length of spawning individuals.

Popu- lation	Standard length, mm average	Gillrakers average	Number of specimens	Scales average	Number of specimens
1	79	38.0	30	76.5	15
2	118	37.1	17	87.4	11
3	120	37.2	100	80.5	100
4	124	25.5	52	83.7	50
5	128	39.0	119	84.1	119
6	129	33.8	194	—	—
7	132	35.7	22	91.2	17
8	136	31.5	8	84.0	6
9	138	30.0	65	—	—
10	138	39.5	163	84.2	163
11	140	35.7	83	—	—
12	142	36.2	9	84.3	8
13	143	33.7	13	95.3	6
14	144	20.0	100	—	—
15	145	34.1	73	91.9	73
16	148	45.0	100	85.5	100
17	155	22.9	15	86.0	15
18	157	38.2	143	89.4	143
19	157	38.4	121	87.8	121
20	158	34.4	70	90.9	70
21	159	35.0	17	87.5	17
22	163	37.1	127	86.2	109
23	166	35.5	8	93.1	8
24	169	37.2	50	94.5	50
25	174	33.2	16	95.7	15
26	175	34.2	17	86.5	17
27	180	34.6	27	88.5	32
28	181	34.1	24	92.8	24
29	183	36.0	58	91.6	58
30	186	36.5	85	83.4	85
31	187	37.1	50	95.3	50
32	205	20.2	23	95.1	23
33	213	23.8	4	91.8	4
34	213	34.9	95	95.8	95
35	216	19.4	32	92.3	32
36	216	32.8	49	99.7	49
37	229	35.8	175	98.4	117
38	230	35.4	5	92.8	5
39	241	29.1	9	95.0	9
40	244	27.7	15	92.2	15
41	257	26.4	30	89.6	30
42	257	29.9	38	95.2	38
43	259	27.1	21	93.1	21

Table 1 (continued).

Popu- lation	Standard length, mm average	Gillrakers average	Number of specimens	Scales average	Number of specimens
44	259	32.6	18	91.8	18
45	261	27.2	51	95.0	49
46	264	27.4	50	93.7	49
47	266	40.6	40	93.4	40
48	267	40.8	52	93.3	52
49	267	26.6	98	93.4	97
50	275	39.2	17	93.0	13
51	283	28.0	75	97.3	71
52	283	31.1	35	95.9	35
53	285	26.4	10	93.8	9
54	286	38.3	24	98.2	24
55	290	24.2	48	96.7	47
56	291	24.8	21	94.4	21
57	294	23.0	30	95.5	30
58	296	36.9	60	93.2	60
59	299	22.6	17	95.6	17
60	299	39.4	48	100.9	48
61	304	31.7	44	98.1	44
62	311	22.4	16	95.9	15
63	312	21.1	35	89.3	32
64	316	21.2	47	93.4	47
65	317	31.3	50	97.0	49
66	317	25.6	22	96.9	22
67	317	23.9	45	94.1	45
68	323	45.3	50	97.8	50
69	324	20.6	22	94.9	22
70	324	19.8	94	95.3	94
71	326	28.7	44	98.9	44
72	328	28.5	30	101.4	30
73	329	19.4	12	97.8	12
74	341	25.1	88	101.3	85
75	344	28.3	73	100.3	57
76	346	20.8	23	89.6	23
77	350	22.3	10	94.4	10
78	355	28.9	40	98.1	40
79	356	27.3	15	95.4	15
80	357	21.3	22	94.8	22
81	359	28.5	98	97.6	98
82	363	29.4	81	97.5	81
83	372	29.8	30	100.2	17
84	379	21.0	25	91.1	25
85	380	40.6	31	95.1	31
86	381	28.8	113	97.1	113
87	383	28.5	25	96.2	25
88	389	23.5	32	94.3	32
89	390	24.8	20	94.7	20
90	402	31.1	14	95.5	14

Table 1 (continued).

Popu- lation	Standard length, mm average	Gillrakers average	Number of specimens	Scales average	Number of specimens
91	403	39.2	21	97.7	21
92	409	27.5	13	98.5	13
93	440	27.2	22	97.4	22
94	441	24.4	26	96.6	26
Totals			4.499		3.896

Table 2. Standard length, gillrakers and scales in populations, selected from table 1 and considered as belonging to one single species, the *storsik*.

Population	Standard length	Gillrakers	Scales
17	155	22.9	86.0
32	205	20.2	95.1
35	216	19.4	92.3
55	290	24.2	96.7
56	291	24.8	94.4
57	294	23.0	95.5
59	299	22.6	95.6
62	311	22.4	95.9
63	312	21.1	89.3
64	316	21.2	93.4
67	317	23.9	94.1
69	324	20.6	94.9
70	324	19.8	95.3
73	329	19.4	97.8
76	346	20.8	89.6
77	350	22.3	94.4
80	357	21.3	94.8
84	379	21.0	91.1
88	389	23.5	94.3
94	441	24.4	96.6

species of whitefish have been selected from table 1 (Tables 2, 3 and 4). The question how the number of scales varies within each such group is now of great interest. The 20 populations of what are probably *storsik* display a correlation coefficient of 0.3786 (P larger than 0.05), the 28 populations of *älvsik* have a coefficient of 0.8050 (P much less than 0.001) and finally the 34 populations of *bläsik* have a coefficient of 0.6694 (P less than 0.001). Two of the three coefficients are thus highly significant, showing that the correlation between body size and number of scales is also valid *within* a group of related populations.

Table 3. Standard length, gillrakers and scales in populations, selected from table 1 and considered as belonging to one single species, the *älvsik*.

Population	Standard length	Gillrakers	Scales
4	124	25.5	83.7
8	136	31.5	84.0
39	241	29.1	95.0
40	244	27.7	92.2
41	257	26.4	89.6
42	257	29.9	95.2
43	259	27.1	93.1
45	261	27.2	95.0
46	264	27.4	93.7
49	267	26.6	93.4
51	283	28.0	97.3
52	283	31.1	95.9
53	285	26.4	93.8
65	317	31.3	97.0
66	317	25.6	96.9
71	326	28.7	98.9
72	328	28.5	101.4
75	344	28.3	100.3
78	355	28.9	98.1
79	356	27.3	95.4
81	359	28.5	97.6
82	363	29.4	97.5
83	372	29.8	100.2
86	381	28.8	97.1
87	383	28.5	96.2
90	402	31.1	95.5
92	409	27.5	98.5
93	440	27.2	97.4

Transplantations

It is difficult to rear whitefish in aquariums to a sexually mature size and it is extremely difficult to do so on such a large scale that many dozens of fish can be obtained for examination and comparison with the variations of natural populations. As the characters used in whitefish systematics are meristic one must work with the average instead of simple qualitative differences. This increases the necessity for making the transplantation experiments on a sufficiently large scale. The best expedient is, therefore, to transplant the individuals from one population to another environment, where they can then be allowed to build up a new population, that can be compared with the mother population. A distinct disadvantage with this method is, of course, that one has not got the environmental factors under control but

Table 4. Standard length, gillrakers and scales in populations, selected from table 1 and considered as belonging to one single species, the *blåsik*.

Population	Standard length	Gillrakers	Scales
1	79	38.0	76.5
2	118	37.1	87.4
3	120	37.2	80.5
5	128	39.0	84.1
7	132	35.7	91.2
10	138	39.5	84.2
12	142	36.2	84.3
13	143	33.7	95.3
15	145	34.1	91.9
18	157	38.2	89.4
19	157	38.4	87.8
20	158	34.4	90.9
21	159	35.0	87.5
22	163	37.1	86.2
23	166	35.5	93.1
24	169	37.2	94.5
25	174	33.2	95.7
26	175	34.2	86.5
27	180	34.6	88.5
28	181	34.1	92.8
29	183	36.0	91.6
30	186	36.5	83.4
31	187	37.1	95.3
34	213	34.9	95.8
37	229	35.8	98.4
38	230	35.4	92.8
47	266	40.6	93.4
48	267	40.8	93.3
50	275	39.2	93.0
54	286	38.3	98.2
58	296	36.9	93.2
60	299	39.4	100.9
85	380	40.6	95.1
91	403	39.2	97.7

must be content with noting the changes of the phenotypes, which can perhaps occur. If a population proves to be constant after a solitary transplantation, this need not signify anything more than that the environmental factors within the lakes are the same. It is no proof that the characters studied are genotypic. If, on the other hand, repeated transplantations to such varied biotops as possible show that the characters studied display a tendency to remain unchanged, this shows that the property has but little capacity for phenotypic variation, especially if other characters are con-

Table 5. Gillraker stability in transplanted populations.

Population No. from Tab. 1	Locality	Number examined	Average number of gillrakers	Transplantation locality	Number examined	Average number of gillrakers	Difference	P.
37	Gimån	175	35.77	Hållsta-lakes	17	36.59	+ 0.82	> 0.05
37	»	175	35.77	Orrån, Sicksjön	36	35.81	+ 0.04	> 0.05
37	»	175	35.77	Svarttjärn, Bräcke	29	37.55	+ 1.78	< 0.001
37	»	175	35.77	Pond, Kälarne	100	35.86	+ 0.09	> 0.05
42	Drögen	38	29.89	Njarven	22	29.59	- 0.30	> 0.05
57	Dellen	30	23.00	Öjungen	40	22.95	- 0.05	> 0.05
60	Stora Gla	48	39.42	Lelången	35	37.51	- 1.91	< 0.001
65	Indal	50	31.32	Pond, Kälarne	38	30.79	- 0.53	> 0.05
68	Uddjaur	50	45.34	Vontjärn, Kälarne	81	44.16	- 1.18	0.01
81	Bure älv	98	28.45	Lajnijaur	32	29.63	+ 1.18	< 0.001
81	»	98	28.45	Brunträsket	50	29.58	+ 1.13	< 0.001
82	Råne älv	81	29.44	Vitträsket	25	27.56	- 1.88	< 0.001

siderably changed at the same time thus indicating great differences in environment.

The following transplantations have been examined and the results summarized, regarding scales and gillrakers, in tables 5 and 6. The population numbers refer to table 1, which gives the mother populations but not their offspring.

Population 37. The locality is the river Gimån, which feeds Lake Idsjön and is a tributary of the great river Ljungan. In Lake Idsjön three sympatric species of whitefish occur, one of which, called *Gimåsik*, makes its way up the Gimån in the autumn for spawning. There has been rather intensive fishing for whitefish during the spawning season for a great many years and this fishing has been described by TOOTS (1949). The further whitefish species in Idsjön are a small-sized population of *älvsik*, which was discovered by TOOTS in 1950 and was previously unknown to the fishermen living round the lake (population 4 in table 1). Finally there is a large whitefish in Idsjön, *storsik*, spawning about Christmas time. Only two specimens of this third species have as yet been examined.

The Gimå whitefish have been the subject of intensive fish culture as the eggs are easily secured in October and November. For many years fry has been produced at the fish hatchery at Kälarne and the fry has been distributed to a great many lakes in the region.

The Gimå whitefish have been successfully introduced in the Hållsta lakes, situated in the neighbourhood, by means of transplantations in the years 1942 and 1944. These have resulted in an extensive population of whitefish, which now spawn in running water between the lakes in October. Other transplantations with unknown material have taken place in the lakes in the

years 1882, 1930 and 1935 but have clearly been unsuccessful, as whitefish were never found afterwards except for an occasional specimen. After the transplantations in the 1940's, on the other hand, the conditions have been quite different. As the Gimå whitefish spawn in running water it is particularly significant that the new population in the Hållsta lakes have retained this habit.

The 17 whitefish from the Hållsta lakes, which have been examined and accounted for in tables 5 and 6, have been caught in 1951 and constitute in all probability the second or third generation in the new environment.

The Gimå whitefish have also during the years 1934—1936 been transplanted to another little lake, Sicksjön, quite near the Kälarne hatching station. In Lake Sicksjön there are two sympatric species of whitefish, *storsik* (population 59 in table 1) and *blåsik*, which has approximately 36—37 gillrakers. The *blåsik* has been examined but is not included in table 1, as a mixed stock containing some known hybrid fish was unfortunately released in the lake in 1945 and these fish have formed shoals with the spontaneous *blåsik*. It has, thus, not been possible to obtain a pure stock of these fish, but as more than 100 fish were examined the figures given for the gillrakers are probably quite reliable.

In a little stream, Orrån, which runs into Lake Sicksjön, whitefish began to appear in great numbers at the spawning season during the latter half of the 1940's. These whitefish spawn in October—November while the spontaneous *blåsik* in Sicksjön were noted for their late spawning season, which did not occur until February. Fishery Assistant E. HALVARSSON has carefully interviewed a number of persons living round Lake Sicksjön and there appears to be no doubt that spawning whitefish were never observed in Orrån before the 1940's and that whitefish never spawned in October—November before that time. As the indigenous *blåsik* still keep to their spawning season in February, a new stock must have come into the lake and this cannot be anything but offspring of the transplanted fry of Gimå whitefish. It is uncertain whether the Gimå whitefish and the spontaneous *blåsik*, which should reasonably be populations belonging to the same species, have given rise to hybrids in the lake. In any case these facts indicate that a certain internal rhythm as regards the spawning season can remain constant on transplantation (cf. the discussion on the stability of the spawning season in SVÄRDSON 1951). The specimens from Orrån in L. Sicksjön, of which an account is given in tables 5 and 6, have been caught on November 12th 1949, and they probably constitute the third-fourth generation of Gimå whitefish in the new environment.

Fry of Gimå whitefish were transplanted in the spring of 1949 in a little lake, Svarttjärn in Bräcke, which is also in the neighbourhood of Kälarne. No whitefish were previously found in the lake. The fry proved to be far superior in growth to the original stock and in the autumn of 1951 a

Table 6. Modification of the number of scales in transplanted populations.

Population No. from Tab. 1	Locality	Number examined	Average number of scales	Transplantation locality	Number examined	Average number of scales	Difference	P.
37	Gimån	117	98.39	Hållsta-lakes	15	93.87	- 4.52	< 0.001
37	»	117	98.39	Orrån, Sicksjön	36	93.94	- 4.45	< 0.001
37	»	117	98.39	Svarttjärn, Bräcke	29	97.03	- 1.36	> 0.05
37	»	117	98.39	Pond, Kälärne	100	92.98	- 5.41	< 0.001
42	Drögen	38	95.18	Njarven	22	97.05	+ 1.87	> 0.05
57	Dellen	30	95.47	Öjungen	40	97.93	+ 2.46	< 0.01
60	Stora Gla	48	100.88	Lelången	35	100.29	- 0.59	> 0.05
65	Indal	49	97.02	Pond, Kälärne	31	85.65	- 11.37	< 0.001
68	Uddjaur	50	97.78	Vontjärn, Kälärne	75	95.33	- 2.45	< 0.001
68	»	50	97.78	Pond, Kälärne	105	92.82	- 4.96	< 0.001
81	Bure älv	98	97.59	Lajnijaur	32	98.16	+ 0.57	> 0.05
81	»	98	97.59	Brunträsket	50	97.82	+ 0.23	> 0.05
82	Råne älv	81	97.46	Vitträsket	25	93.76	- 3.70	< 0.001

sample of these fish was taken, which is included in tables 5 and 6. Finally nearly every year fry of Gimå whitefish were reared to one summer old fish in ponds at Kälärne hatching station, and a sample of such one summer old fish from the autumn of 1945 has been examined. Thus there is a total of four samples of Gimå whitefish in other waters than the Gimån, all of which include non-selective material, that is to say no choice has taken place regarding the mother fish in the Gimån or the fry that have been transplanted.

Altogether 175 specimens of the Gimå whitefish have been examined as regards gillrakers and 117 as regards the number of scales along the side of the body. These fish came from the traditional fishing and were taken without selection in 1947, 1948 and 1950.

Population 42. This population is spontaneous in Lake Drögen, situated approximately 25 km south of the town of Linköping in southern Sweden. The lake is oligotrophic and is one of the few lakes in that region, which still have a stock of whitefish. Apart from the transplanted population there is another species in L. Drögen, *storsik*, but only three specimens of this form have been examined and it is obviously rare. The Drögen whitefish were transplanted to Lake Njarven, 25 km further south, in the spring of 1939, when 175,000 fry of Drögen whitefish were released in Njarven. No whitefish were found there previously. Samples were collected from both Drögen and Njarven at the beginning of December, 1949 and 1950. The Njarven whitefish probably constituted the second or third generation since the transplantation.

Population 57. Not far west of the town of Hudiksvall, about the middle of the Swedish Baltic coast, lies a large lake, Dellen, which is noted for its

population of large-sized whitefish. These whitefish as well have been transplanted to other localities and one of them could be used in this connection. The case in question is a transplantation in Lake Öjungen, which is situated about 70 km southwest of Dellen. There 247.000 newly fertilized eggs from Dellen were transplanted in the year 1920 and since then no further transplantations have taken place. This transplantation gave rise to an extensive population of whitefish, the individual fish being remarkable for an extremely rapid rate of growth especially during the first ten—fifteen years. Now the rate of growth has become about the same as in L. Dellen or perhaps somewhat slower. Samples of Dellen whitefish and Öjungen whitefish were obtained in November 1948. The Öjungen whitefish were probably the fifth—sixth generation in the new environment at that time.

Population 60. This population derives from the west of Sweden, more exactly from Lake Stora Gla, which lies 20 km south-southwest of the town of Arvika, quite near the Norwegian frontier. It is likely that there is another sympatric species of whitefish in Stora Gla, because this is the case in some of the neighbouring lakes. 268 adult whitefish caught in nets were transplanted in the autumns of 1925—1927 to one of the lakes in the region, where whitefish were not previously to be found. This gave rise to a new stock in that lake, which is called Lelången. The samples, of which an account is given in tables 5 and 6, have been captured in the lakes during the spawning season, November, in the years 1949 and 1951. The Lelången whitefish probably constitute approximately the fifth generation.

Population 65. The locality is Indal in the river Indalsälven, where whitefish from the Baltic enter the river, moving upstream for about 50 km to spawn. These whitefish are fairly large and the river is well-known for its whitefish fishing season in October—November. Eggs have been secured and hatched at the Kälärne station. In tables 5 and 6 a sample of one summer old fish is included, which were raised at Kälärne in the year 1947. The 50 fish from the spawning population at Indal were taken on November 21, 1950.

Population 68. The transplantation of *aspsik* from Lake Uddjaur in Arjeplog in northern Sweden down to the little lake Östra Vontjärn at Kälärne has already been described (SVÄRDSON 1950).

Population 81. The locality for this population is the river Bure near the town of Skellefteå, and the transplantation of this whitefish to L. Lajnijaur and L. Brunträsket in Malå Parish has been previously described in detail (SVÄRDSON 1951).

Population 82. The River Råne, which flows into the Gulf of Bothnia about 30 km north of the town of Luleå, is visited every autumn by shoals of whitefish going up the river to spawn, as they do in the mouths of so many other rivers along the Baltic coast of Sweden. Similarly to the Bure whitefish further south this Råne whitefish has been the subject of a great number

of transplantations in fresh water, in spite of its being a whitefish that normally lives in the sea. The reason for this is primarily that it is so easy to obtain large amounts of newly fertilized spawn in the autumn. One day in the autumn of 1951, for instance, more than 1,000 kg of whitefish were caught at the fishery carried on for the purpose of obtaining eggs. In a small lake in the neighbourhood, Vitträsket, where no whitefish were previously to be found, fry of Råne whitefish were transplanted for some years at the beginning of the 1940's, giving rise to a population of very large-sized fish. A sample of this transplanted Råne whitefish from L. Vitträsket was obtained in October 1949 and samples of Råne whitefish were procured in October 1949 and 1951. The whitefish, that were examined, constitute the first generation in the new environment.

Altogether there are 12 cases, where the constancy of the gillrakers could be studied, and 13 cases, where the stability of the number of scales along the side of the body could be tested (Tables 5 and 6). The transplantations have comprised the four species of whitefish to be found in Sweden, namely *storsik*, *älsik*, *blåsik* and *aspsik*. Transplantations have been made of stocks from both the south and north, the east as well as the west of Sweden. The transfers have been both short distances, to lakes in the neighbourhood, and long, corresponding to one third of the total length of Sweden from north to south. The new populations studied have partly consisted of the transplanted fish themselves, partly of their offspring up to the fifth or sixth generation.

The differences between mother and daughter populations, as illustrated by samples taken in the manner just described, may be attributed to several factors:

1. Sampling error, due to selective net-fishing, when the mother or the daughter population was sampled.
2. Sampling error, due to relatively small numbers of parent fish, when fertilized roe was secured from the mother population.
3. Natural selection within the daughter population before time of sampling.
4. Environmental non-genetical modification of the daughter population.
5. Sampling error, due to relatively small numbers of fish, when the mother or the daughter population was sampled.

Obviously it is impossible to analyze in detail the degree of non-genetical environmental modification of the daughter populations unless all factors are taken into account. The sampling error, when the mother and daughter populations were sampled (point 5), can be calculated and in tables 5 and 6 the probability (P) for chance fluctuations alone being responsible for the difference found has been included. Out of the twelve transplantations, six display a difference so great as to give a P-value of 0.01 or less with regard to the gillrakers. This means that the difference found in six cases is probably

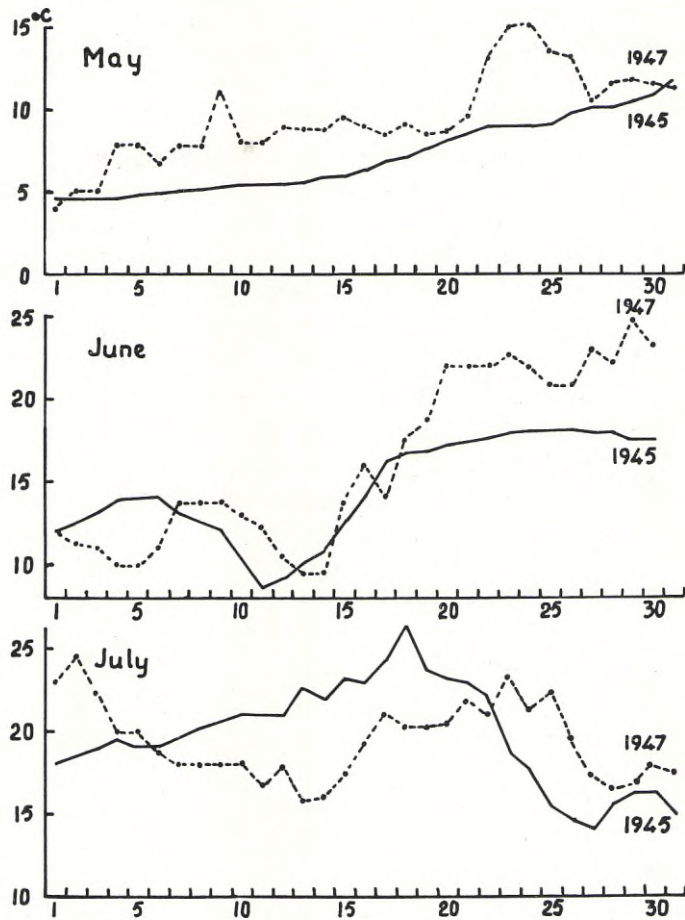


Fig. 1. Water temperature of the ponds at Kälärne hatching station.

solely due to general sampling errors and no real change has occurred in the transplanted population. The six remaining cases, however, show differences which cannot be attributed to variation according to point 5.

Natural selection could alter the gillraker frequencies within a population by differential mortality or differential fertility. The differential mortality should reasonably occur in the fry or fingerling stages, but it was found that this had probably not taken place in the case of Bure whitefish transplanted to Lake Brunträsket (SVÄRDSON 1951). Differential fertility on the other hand seems very probable, as a consequence of differential growth of individuals with different numbers of gillrakers. The better the growth, the earlier maturity is attained, the greater is the number of eggs laid and the larger are the eggs. This must establish differential growth as the most important factor in natural selection.

Out of the six changed daughter populations four were first generation fish,

where natural selection could only work by differential mortality in the earlier stages and it is, therefore, not very probable that it is the responsible factor. The change observed could, accordingly, be attributed to one or both of the two first listed sources of variation or be referred to non-genetical environmental modification. Selective fishing may occur and is illustrated below (*vide infra*) and sampling error, when the fertilized roe was secured, may have occurred too, which is further indicated below when an experiment on artificial selection from one population is discussed. There is good reason to think that environmental modification of the gillraker apparatus is slight or non-existent. This cannot be proved with the methods hitherto used. Even if this source of variation should be solely responsible for the change observed, which is probably not the case, the extent of this change is still small, since no daughter population deviates from its mother population by more than two units. This is a very slight change, when the normal variation within one homogenous population is about ten units or even more.

When the Bure whitefish was transplanted to Lake Brunträsket and Lake Lajnijaur an increase in the gillraker number occurred, which could not be attributed to sampling error or natural selection. The change was, therefore, referred to environmental modification (SVÄRDSON 1951). When the two further sources of variation are taken into account, however, this conclusion is found to be invalid. The increase was then thought to be brought about by the transfer of the whitefish from the sea to fresh water. The Råne whitefish, however, which has also been transplanted to fresh water, has acquired a smaller number of gillrakers (Table 5) and this occurrence strengthens the invalidity of the first interpretation. Water quality cannot, thus, be said to modify the gillraker apparatus.

It has previously been shown (SVÄRDSON 1950) that the gillrakers in whitefish fry have not appeared in their full numbers when the fry have a total length of 70 mm or less. In table 5 are included two cases where the fry have been 100—120 mm long, total length (Gimå whitefish and Indal whitefish reared in ponds in Kälarne). Both of these display an unchanged number as compared with the parental populations, for which reason the additional conclusion can be reached that although the gillrakers have not appeared in their full numbers at a total length of 70 mm, this is the case when the fry have attained a size of 100—120 mm.

In table 6 is assembled the information available regarding the constancy in the number of scales along the side of the body. No difference has arisen in five cases, while there is such a difference in eight cases (P less than 0.01). Both increases and decreases are to be found, although the decreases predominate, especially as regards transplantations of Gimå whitefish. The differences between the parent stock and the daughter stock are very decided in this respect and in one case the difference amounts to more than 11 scales on an average. Since MOTTLEY (1934) proved that high water temperature

could reduce the number of scales in *Salmo kamloops* with 10—15 units one could expect that a transplantation of whitefish from natural lakes to the comparatively warm ponds at Kälärne would reduce the number of scales. This has proved to be the case.

Whitefish from the Gimån and from Uddjaur, belonging to different species, have both in their home lakes approximately 98 scales on an average but both got that number reduced to 93, when their fry in the summer of 1945 were reared in ponds at Kälärne. On the other hand whitefish from Indal, which has 97 scales in the Indalsälven, got only 86 scales at Kälärne, when it was reared there in the summer of 1947. Both the summers of 1945 and 1947 were exceptionally hot (detailed discussion on the subject in SVÄRDSON 1951) and the temperature in the ponds at Kälärne shows (Fig. 1) that May and the latter half of June 1947 provided unusually warm water. The fry, after it is hatched, is usually put out into the ponds in the first week or weeks of May and it normally passes its scale-developing period (total length 2—4 cm) in June. Therefore, in this case, there can hardly be any doubt that the exceptionally small number of scales in the fry of Indal whitefish at Kälärne in the year 1947 was occasioned by warm water and probably by the heat-wave, which prevailed for almost three weeks starting from the middle of June.

The reason that the Gimå whitefish, as is shown in table 6, after every transplantation got fewer scales along the side of the body than it has in its home lake can be attributed to the fact that in the Gimån it spawns early in the autumn, consequently hatches relatively early in the spring and, thus, passes the sensitive stage in cold water. In relation to the small size of its body, the Gimå whitefish has also an unusually large number of scales. It is, therefore, quite natural that more often than not it will show a reduction in the number of scales on transplantation.

The Dellen whitefish, which was transferred to Öjungen, has got more scales than in its home lake. This agrees with the fact that Öjungen, which lies at a greater height above sea level, grows cold earlier, thereby causing the whitefish to spawn earlier in the autumn (there is a difference of at least a week between the height of the spawning season in the two lakes) and as a consequence of the spawning-time the whitefish in Öjungen gets a greater number of scales. Thus, to a considerable extent, the scales seem to be a morphological consequence of purely ecological factors.

As a summary of the results of the transplantations, it can be said that:

- (1) the gillrakers have all appeared when the young whitefish have attained a total length of 100—200 mm,
- (2) on transplantation to a new lake the number of gillrakers remained entirely unchanged or changed to a very slight extent, in no case exceeding 2 units on an average,

- (3) on transplantation from one environment to another the number of scales can be very considerably changed, up to 11 units in one case. This is correlated with the temperature during the time the scales were developed and a high water temperature gives a small number of scales.

Evidence of Selection Experiments

In order to shed still further light on the genetic nature of the gillrakers, experiments were made in the autumn of 1950 with artificial selection. The idea was, moreover, to demonstrate how local populations of one and the same species can get different numbers of gillrakers.

Mr. HENDRIK TOOTS succeeded in finding after a lengthy search in the Gimån two pairs of fish, which were suitable as parents for a selected generation. Both the fish in one pair had 32 gillrakers, while both fish in the other pair had 41 gillrakers, counting as usual on the first left arch. The females' spawn was fertilized with the males' milt and the spawn was taken as soon as possible to the Kälarne hatching station, where Mr. HALVARSSON took charge of the spawn. The hatching in the spring of 1951 was successful and two small lakes without whitefish were chosen for rearing the fry. The fry from the 41-pair was placed in L. Kvarntjärn and the fry from the 32-pair in L. Svarttjärn in Kälarne (not identical with L. Svarttjärn in Bräcke mentioned earlier). Mr. HALVARSSON succeeded in the autumn of 1951 in catching 40 one summer old fish in Kvarntjärn, that were then 120—150 mm long, while no fish were caught in Svarttjärn until the break-up of the ice in the spring of 1952, when a total of 42 specimens, approximately 200 mm long, were captured. Incidentally it can be mentioned that the fish in Svarttjärn at the age of 1 year were practically the same size as the Gimå whitefish first attain at 4—5 years of age. The extraordinary plasticity of their growth has previously been discussed in full detail (SVÄRDSON 1949, 1950, 1951).

The result of this selection experiment was interesting. While the Gimå whitefish have 35.77 gillrakers and a total known variation of 30—42, the progeny of the 41-pair have 38.28 gillrakers with a variation of 35—42 and the progeny of the 32-pair have 33.43 gillrakers with a variation of 27—38. The variation within the three populations is illustrated in fig. 2 (Fig. 2). With the exception of a single fish with 27 gillrakers all the young fish had numbers, that lie within the variation limits of the parent stock. Both the selected populations diverge further from the parent population (2.51 resp. 2.34) than *all* the transplanted stocks described in table 5. The divergencies in both directions are very positive statistically.

This experiment shows that in one single generation, with strict selection, from a homogeneous population two populations can arise that differ from

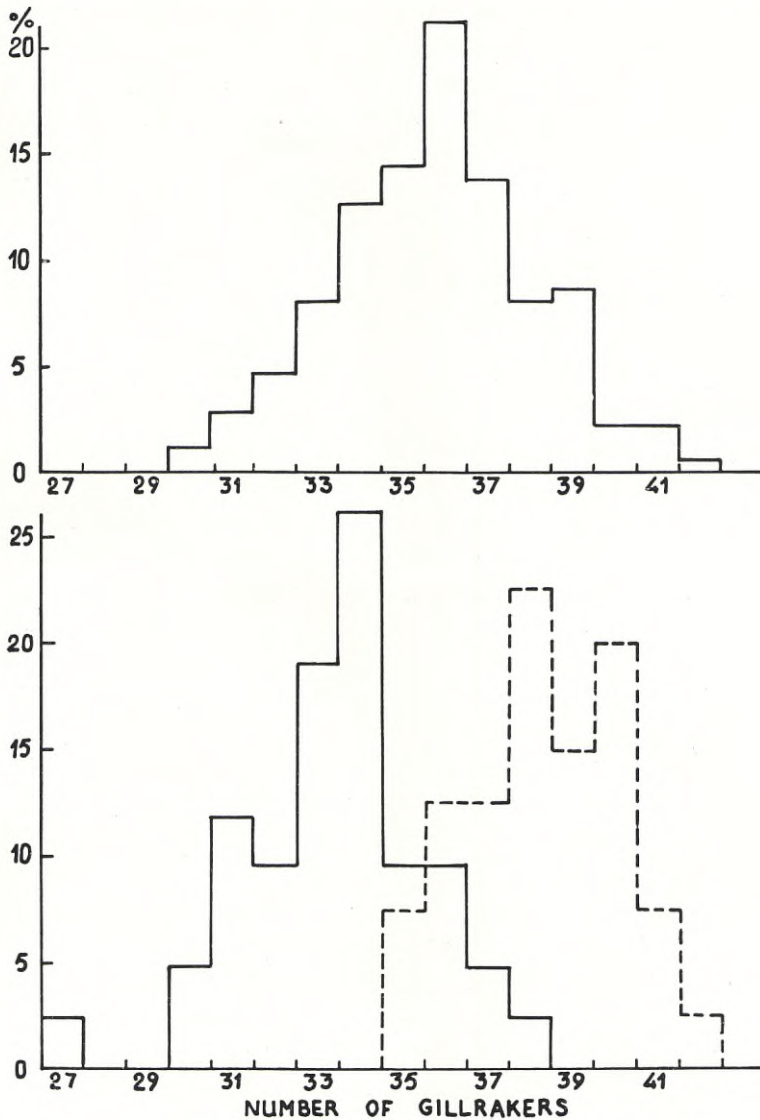


Fig. 2. Frequency of gillrakers of the Gimá-whitefish (above) and of two groups of fish, being progeny of selected pairs. Both fish in one pair had 41 gillrakers, the other 32 gillrakers.

one another with almost five units in the average number of the gillrakers. When it is a question of referring a local whitefish population to a certain species, one must, therefore, not rely too implicitly on the average number found for the gillrakers. As is the case with other characters, which are based on polygenes, a continued selection in both directions should be able

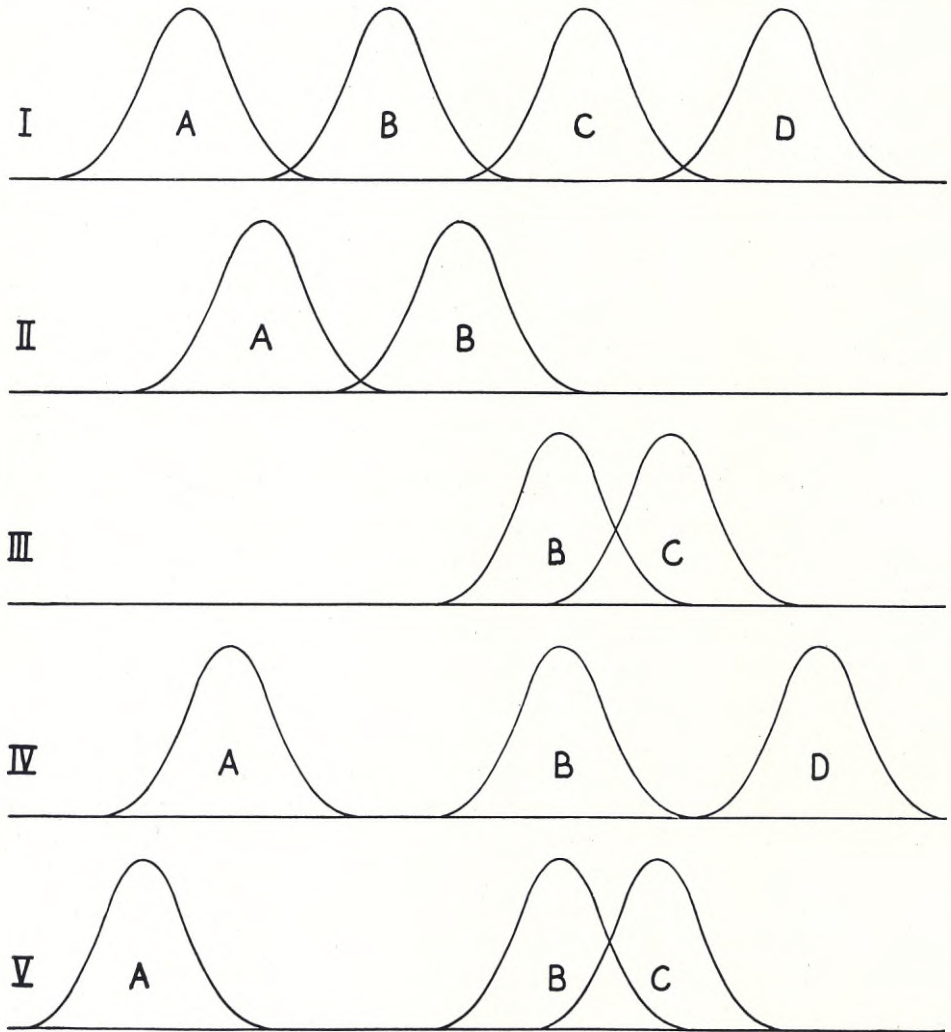


Fig. 3. Illustration to the geographical subspeciation in *Coregonus*. The four sympatric species A—D in lake I are very difficult to identify in the lakes II—V, due to their evolution of local forms. As long as only the gillrakers are taken into account the local population can most often alternatively be referred to one of two different species.

to produce Gimå whitefish with still more divergent numbers. Some indications show that local populations of one species can differ so much as to almost mask the differences between different species. The taxonomic difficulties, which the *Coregonus* species display, are partly caused by the excessive geographical differentiation they have undergone since their invasion to their present distribution area. Fig. 3 illustrates how the evolution of local populations complicates the identification of species.

Evidence from Hybrids

Artificial hybrids. Further evidence as to the gillrakers is obtained from hybrids. In Lake Dikasjön in Wilhelmina Parish there are two sympatric species of whitefish, *storsik* and *blåsik* (population 56 resp. 19 in table 1) and they spawn near to one another and at almost the same time in October. At the request of my colleague Dr. ERIC FABRICIUS a crossing of these two species was made in the autumn of 1950 by Fishery Assistant BIRGER AHLMÉR, the spawn of the large-sized *storsik* being fertilized with milt from the stunted *blåsik*. The fertilized spawn was taken to Semlan fish hatchery, where Fishery Assistant H. ANDERSSON saw to its hatching in the spring of 1951, the releasing of the fry in a little lake, Kotjärn, that was free from fish, and afterwards the capture of one summer old fish in the autumn of 1951. Altogether 20 fish were caught then with a total length of 110—120 mm. They were, consequently, so big that the gillrakers should be fully developed.

The *storsik* in Dikasjön has an average of 24.8 gillrakers with a known variation of 22—27, while the average for the *blåsik* is 38.4 with a variation of 31—44. The hybrids had a variation span of 30—35 and an average of 32.0. They were, accordingly, quite intermediary.

The transfer of *storsik* from Uddjaur to Kälärne 1944—45 has previously been described by the present writer (SVÄRDSON 1950). Later information has, however, shown that this transplantation, which entailed relatively great changes, then interpreted as environmental modifications, is uncertain and it has therefore been removed from tables 5 and 6, which summarize all transplantations studied by the author up to the present. The uncertainty has arisen owing to the probability that hybrids of *storsik* and *aspsik* have unintentionally been produced at the spawn collection, which should only have included the *storsik*. The person, who collected the samples failed to distinguish some *aspsik* from the dominating *storsik* and the author did not know then (1944) that *aspsik* could still be capable of spawning as late as the time when the *storsik* spawns. This has, however, been proved very conclusively in the autumn of 1950, when ripe specimens of both species were collected simultaneously and at the same spawning-ground at the end of December in Uddjaur. It is now quite evident that the spawn collection in 1944 unfortunately produced hybrids.

At the same time new material, previously stored at Kälärne, has become available for study, which alters the situation as far as this question is concerned. A survey of the material is given in table 7.

The fry, hatched in the spring of 1945, was released in ponds at Kälärne and also in a small lake, Ilvåstjärn, with no fish. The fish were too small the first summer to have got the final number of gillrakers. The parental species, the *storsik* of Lake Uddjaur, has 19.8 gillrakers on an average and a known variation of 16—27 (population 70 in table 1). This was exceeded in the two

Table 7. Evidence of unintentionally produced hybrids between *storsik* and *aspsik* (see text).

	Number of gillrakers															Total number of examined specimens	Average					
	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32			33	34	35	36	
2 summers old																						
pond, Kälarne	5	3	11	8	8	7	3	2	—	—	—	—	—	1	1	1	—	—	—	50	21.80	
Ilvåstjärn 1947—																						
1948	—	—	1	2	3	—	1	5	6	4	5	4	7	6	4	—	4	—	2	54	28.31	
Ilvåstjärn 1949—																						
1951	—	—	3	5	7	13	4	14	8	4	2	—	—	—	1	—	1	—	62	24.23		

summers old fish and some of these definitely had much higher numbers, far exceeding the range of the parental species. These fish must be hybrids *storsik* × *aspsik*. In Lake Ilvåstjärn the catch the first years gave gillraker counts much higher than expected, in later years, however, somewhat lower numbers but still far higher than the true *storsik*. The three groups are all significantly different from each other (*P* less than 0.001). There is the theoretical possibility that someone has illegitimately released foreign fry in Lake Ilvåstjärn in the spring of 1945, which has shoaled together with the *storsik* and the hybrids. All fish examined were the same age and hatched in spring 1945. Nevertheless, the difference between the first and the later catches in Lake Ilvåstjärn must be due to sampling error. Most probably fishing has been selective, taking in the first years preponderantly fish with a large number of gillrakers (hybrids) and later on more and more fish with lesser numbers (true *storsik*). It can be seen from the length data that the growth of the fish has been dissimilar, the hybrids having the better growth. This can be due to hybrid vigour or the fact that bottom organisms are extremely few in Lake Ilvåstjärn, plankton being the only available food. It seems reasonable to suppose that fish with a larger number of gillrakers could manage this plankton diet better. Growth was extremely poor in all the specimens, though poorest in those with few gillrakers.

This experiment, which was started to provide information about the stability of gillrakers in different environments, instead indicated intermediate gillraker number in hybrids and demonstrated the importance of selective fishing.

Natural hybrids. Further facts concerning the production of natural hybrids have been obtained. The previously mentioned whitefish in Lake Dellen, which were transplanted to Öjungen, have also been transferred to another lake, near Dellen, named Tandsjön. No whitefish were previously to be found in Tandsjön. Then the small whitefish, *Coregonus albula*, from Lake Siljan in Dalarna were also transplanted there but another species came at the

Table 8. Evidence of spontaneous hybrids between *storsik* and *blåsik* in Lake Tandsjön.

	Number of gillrakers																				Total number of examined specimens			
	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37		38	39	40
<i>Blåsik</i> , Siljan ..	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	95
<i>Storsik</i> , Dellen (and Öjungen)	1	4	2	10	9	15	12	12	4	—	—	1	—	—	—	—	—	—	—	—	—	—	—	70
Whitefish, Tandsjön	—	1	1	1	3	8	5	10	2	2	3	3	2	—	—	1	2	—	—	—	—	—	—	44

same time, the *blåsik* from Siljan locally known as »ryssing» (population 34 in table 1). The fry of *Coregonus albula* contained some fry of *blåsik* as well. The *storsik* from Dellen were transplanted there in 1942 and the *blåsik* from Siljan came into the lake as early as 1933. A sample of whitefish from Tandsjön in November 1951 shows that hybrids *storsik* × *blåsik* had spontaneously arisen in the lake (Table 8).

It is apparent from the distribution of the gillrakers in the whitefish in Lake Tandsjön that the majority of the fish have more or less intermediary number of gillrakers. Three specimens with 34—35 gillrakers are probably pure *blåsik*, similarly it is probably that some of the fish with a small number are pure *storsik*. It can, therefore, be said that in Tandsjön there are both *storsik*, *blåsik* and hybrids between them. The growth of the *blåsik* has always been better in Tandsjön than in Siljan, but nowadays the growth is still better, making it difficult for the fishermen to distinguish the »small» *blåsik* from the large-sized *storsik*. This change of growth rate indicates inversed population changes.

It is of great interest that Fishery Assistant HARALD FORSLIN, who kindly helped to reveal the history of different transplantations into Lake Tandsjön, states that whitefish spawn collected in Tandsjön invariably gives poor results. The newly fertilized spawn begins to die a few days after fertilization and the mortality is very great. This corresponds to cytological observations made on fish hybrids (SVÄRDSON 1945).

III. Discussion

Scales. The number of scales along the body has been considered for a long time of appreciable taxonomic importance, not only in Coregonid fishes. It has been presumed that this character is not modified by different environments but that the dissimilarities observed between populations indicated real genetic differences. Almost all authors within Coregonid research have accorded a certain importance to the number of scales and the majority

of descriptions of new species and subspecies give the known range of variation. KOELZ (1931) used this character to distinguish between different subspecies within the species *Leucichtys artedi* and HUBBS and LAGLER (1947) in their key to the Coregonids of the Great Lakes Region use the number of scales in some cases to diagnose both subspecies and species. BERG (1948) in his survey of the Russian whitefishes also used the number of scales for the diagnoses.

The study of the variation of the scales, recorded in this paper, proves that the number of scales can be reduced with ten units as an environmental modification depending on changed temperature conditions. This means that substantially different numbers of scales in allopatric populations can depend solely on the ecological conditions, especially the time for spawning in the autumn and the warming of the water in the spring. In the main, populations that spawn early in the autumn get many scales, as they are hatched early in the spring. Conversely populations that spawn late in the autumn or during the winter get a small number of scales. But *within* the same population the annual variations in the scales seem to be very slight. Annual fluctuations in the water temperature seem to result in altered speed in development. This has previously been demonstrated in the case of the whitefish in Lake Stora Skeppträsket, where a warm year (1947) did not yield a smaller number of scales than cooler years (SVÄRDSON 1951). The interpretation given then is supported by the following new facts: two samples of *blåsik* from Lake Siljan, taken 1948 and 1950, both had an average of 95.8 scales. Two samples of *älvsik* from the River Råne, taken 1949 and 1951, had an average of 97.6 resp. 97.4. The *storsik* in Lake Uddjaur had 95.0 scales in a sample from 1944, and an average of 95.5 in a new sample from 1950. Four samples of *storsik* from Lake Brunträsket from the years 1948—1951 had averages of 94.3, 93.8, 94.4 and 92.9. The differences are everywhere insignificant.

This means that the number of scales can contribute to distinguish between different sympatric populations. If specimens of two or more different species have been obtained in the same nets, the scales are of some importance in separating the species. It must not, however, be confused with genetic differences and must not be used in comparing allopatric populations.

Even if sensitivity to temperature greatly reduces the importance of the character in systematics, it becomes still worse when the other modifying factor is taken into consideration. This factor was earlier outlined (SVÄRDSON 1951) but in the present paper it has been definitely demonstrated that well-grown populations have more scales than populations of stunted whitefish. It probably depends on large-sized whitefish laying bigger grains of spawn with bigger embryos and getting bigger newly-hatched fry. A large and a small baby fish seem to get a different number of scales even if they live in the same water, the bigger fish simply »having room» for more scales

along the side of the body. This can also be expressed by saying that the aptitude for growing scales is more fixed in size than the body of the baby fish.

This second modifying factor is responsible for the greater part of the spontaneous variation, which the natural stocks show in this character. Local populations of *blåsik* (table 4) can have such extremely different numbers of scales as 76.5 resp. 100.9 on an average. Such a difference far exceeds that used in the literature to separate both subspecies and species. But when allopatric populations are concerned no taxonomic importance can be given to the number of scales, because the entire variation found or an unknown part of it can and does depend on environmental modification. No support whatsoever has been forthcoming for the theory that the different numbers of scales in allopatric whitefish populations are genetically determined. It is dependant on the enormous environmental variation found in the growth, which has been demonstrated times without number, not least by the fishermen themselves.

It might be added that some other meristic characters, especially the number of finrays and the number of vertebrae, are probably capable of modification to the same marked extent. This has been found as regards finrays during the transplantations reported in this paper. The change which occurs when a population is transplanted to a new environment is of the same order as the differences found between local populations. The vertebrae has not been studied by the present author. VEDEL TÅNING (1952) has summarized the experimental evidence on this subject in trout and the environmental modification is very marked. It is notable that VEDEL TÅNING finds the size of the egg and the fry having no demonstrable influence on the number of vertebrae. In this respect, therefore, a difference seems to exist between the numbers of scales and vertebrae.

The stability of the scales in the different year classes of one and the same population makes them suitable to use as a *method of marking*. On certain occasions it is desirable, for different fishery-biological investigations to decide if the release of fingerlings contributes to the numerical strength of adult fish in the population. Fin-cutting has been the method used for mass marking. The disadvantages with this method, primarily the uncertainty as to whether the fish with cut fins are entirely equivalent to and capable of competing with the unclipped specimens, are not present with the scale method. An advantage is also that it is possible to mark unlimited numbers of young fish at one time during the course of a few weeks by subjecting them to abnormal temperature (high or low depending on whether the stock in question has an unusually large or small number of scales). The Indal whitefish at Kälarne in 1947 (table 6) displayed so low numbers of scales that 80 % of the fry were completely outside the extreme minimum limit for the natural variation of the Indal whitefish in the river. This means,

therefore, that 80 % of the fry were accidentally marked, so that it would have been possible to identify them as adults even if they had then lived for the later part of their lives in the normal environment, that is to say in the river and the Baltic Sea.

Gillrakers. NÜSSLIN (1882) was the first to diagnose the different species of whitefish by the number and length of the gillrakers. NÜSSLIN also clearly understood how great individual variations could occur in several of the systematic characters then employed and what limited value descriptions, based on such properties, really had. Practically the entire range of variation in the number of gillrakers was discovered by NÜSSLIN, who could thus prove how very extreme values, indicating profound differences in feeding and ecological habits, could be found in forms which earlier authors had grouped in one single species on account of purely external similarities. Then THIENEMANN in a number of papers (literature in THIENEMANN 1950) continued and built up an examination scheme, which was entirely based on the number and relative length of the gillrakers. THIENEMANN was later followed by several authors.

Since THIENEMANN (1912) described the alleged rapid change in the gillrakers of the whitefish introduced into Laacher See, the curious situation arose that THIENEMANN, who personally considered the gillrakers to be more or less capable of modification, in spite of this claimed that they were the best character in separating the different species of whitefish from one another. WAGLER, on the other hand, endeavoured in a series of papers (WAGLER 1927, 1937, 1951) to show that the Laacher See whitefish had not changed but that a misunderstanding had arisen regarding the origin of the material. WAGLER accordingly asserted that the gillrakers were constant but in spite of this he considered them not particularly important when it is a question of diagnosing different species. WAGLER tried instead to find a system where the growth, that is to say the notoriously most modifiable of all the characters studied, was made the basis for the diagnoses.

Now it is quite obvious that the Laacher See whitefish cannot be quoted as a proof that the number and form of the gillrakers are highly modifiable. THIENEMANN (pers. comm.) has also admitted this. KREITMANN (1929) claimed that the gillrakers could be modified but his result has been shown by DOTRENS (1950) to depend on a mistake. SURBECK (1921) is another author, who is quoted as having proved the capacity for modification of the gillrakers. His material was, however, very uncertain and the transplantations backwards and forwards between the Vierwaldstättersee and the Sempacher See can very well — according to what we now know — have given rise to hybrids. Thus SURBECK's data do not prove anything at all. OTTERSTRÖM (1922) compared whitefish from fresh and brackish water in Denmark and found a greater number of gillrakers in the whitefish in fresh water. OTTERSTRÖM's data depended, however, on the Baltic whitefish having

fewer gillrakers than the species which lives in the adjacent fresh water. This will be demonstrated in a future paper in this series. OTTERSTRÖM cannot, accordingly, be cited either as an authority on the plasticity of the gillrakers.

All the data, which have been cited in the literature up to the present in support of the opinion that the gillrakers are not constant, thus depend on a misunderstanding, confusion or misinterpretations. Against these can, moreover, be marshalled a number of transplantations, partly made to ponds and thus under considerably better control, where no change occurred, apart from it being shown that young fish do not get the number of the adult specimens until they have attained a certain size. THIENEMANN (1915), FREIDENFELT (1933), JÄRVI (1940) and WIESE (1938) have thus shown stability in the gillrakers on transplantation. Wiese's material, in particular, is very extensive and convincing.

To this can now be added the 12 transplantations studied by the present writer showing that the number of the gillrakers — if no deliberate selection took place on transplantation — remains constant. A change of ± 2 units is not exceeded.

The selection, which was made on the Gimå whitefish and which resulted in the two selected groups differing from each other by almost 5 gillrakers, as well as the fact that hybrids have intermediary numbers show that the number of the gillrakers is regulated by a number of polygenes. It is thus possible to say that the long discussion on their taxonomic value can be concluded. The gillrakers are the only character yet found whose variation in the whitefish has been proved to have a hereditary foundation. Consequently this character should be used as a basis for the diagnoses.

Ranking of populations

The number of the gillrakers has, in principle, nothing to do with the question of how the whitefish forms should be understood. They are understood by the present writer as a number of sympatric cryptic species, each composed by a great number of geographical subspecies, whose morphological variation may overlap the slight morphological differences between the species.

The conception of species is biological. WIDEGREN (1863) has expressed himself in this question in a more »modern» way than the majority of his successors. He disputes with SVEN NILSSON and points out that the morphological differences are often slight between the forms of whitefish but that regard must be paid to the biological conditions. On page 59 he says (translated from Swedish by the present writer): ». . . the closely related forms, which have been assigned by NILSSON to the same species, keep themselves, however, in the same lake and under the same natural conditions, apart from one another, spawn at somewhat different times etc. all of which,

in addition to the morphological differences to be found, confirm that they are in reality different species.»

As yet definite knowledge has not been reached experimentally concerning the sterility in hybrids between the different species of whitefish. The heavy mortality of whitefish roe, secured in Lake Tandsjön from hybrids, reported in this paper, indicates however that a sterility barrier may exist between the species. Similarly indirect evidence is to be found in the same direction. In Lake Uddjaur the samples have shown that one can probably reckon with a certain new production every year of F1-hybrids between *storsik* and *aspsik*. These should be identical with the »albask» recognized by the inhabitants, which are rare, large in size and have never been found forming a stock or with any known spawning-ground. Such a large-sized »albask» has been examined by the present writer on the spot in 1949 and it had 30 gill-rakers, which is a likely number for a hybrid fish but not for any of the known species. Consequently, if every year F1-hybrids are produced anew, but, in spite of this, they remain rare and at the same time the range of variation for *storsik* and *aspsik* keeps constant, the only conclusion can be that these hybrids are sterile or in any case selected against. Similarly in Lake Siljan a number of F1-hybrids are probably produced every year between the three sympatric species *storsik*, *älvsik* and *blåsik* (populations 69,75 resp. 34 in table 1) but in spite of this the species have remained intact for more than two hundred years (SVÄRDSON 1951). The whitefish hybrids are very likely a parallel to the occurrence of sunfish and sucker hybrids in North America or the Cyprinid hybrids in Europe (HUBBS and HUBBS 1933, HUBBS *et.all.* 1943). For the ichthyologists the occurrence of *Coregonus* hybrids adds to all other difficulties of this group of fishes, i.e. the strong environmental modification and the pronounced geographical subspeciation.

IV. Summary

1. In this paper an account is given of 94 spontaneous whitefish populations from the whole of Sweden with regard to the gillrakers and scales along the side of the body. A positive correlation exists between the average body length of the population and the number of scales. An inverse correlation was found between the length of the body and the number of gillrakers. If the populations are grouped in probable species, based on gillrakers and the knowledge of how they behave towards sympatric populations, there is still a positive correlation between size of body and number of scales.
2. On transplantation the gillrakers in twelve cases remained unchanged or diverged from the parent stock with less than 2 units on an average. The largest and smallest deviations were found in the two transplantations from the longest time ago, that is to say where the daughter stock had

been isolated for the greatest length of time, corresponding to 5—6 generations. The number of scales, on the other hand, sometimes shows a decided divergence on transplantation. Removal to a warm pond has in one case entailed a reduction of 11 units.

3. After individual selection of extreme parent fish in a well-observed population of whitefish, two groups of offspring were obtained, each of which differed by more than 2 units from the parent stock in regard to the gillrakers. In one generation two populations were thus obtained, which differed from one another by almost 5 units.
4. Artificial and spontaneous hybrids have an intermediary number of gillrakers. There was a high rate of mortality in spawn from a lake with a large number of spontaneous hybrids.
5. The number of scales along the side of the body depends on (1) the size of the mother fish's body and (2) the ecological habits of the population, that is to say the relation of the spawning season to the warming of the water, the general appearance of the lake basin and its geographical position. Both these non-genetic modifying factors limit the value of the character to usage in identifying sympatric populations only. For allopatric populations the scales have no taxonomic significance. Their sensitivity to temperature makes them suitable for using as a cheap and harmless method for mass marking.
6. The number of gillrakers is regulated by polygenes and is the only character so far used in Coregonid taxonomy, whose variation is proved to have a hereditary basis. The capacity for environmental non-genetic modification is very slight or non-existent. Allopatric populations may have different numbers of gillrakers though they belong to the same species. The genetical adaptation to local conditions is primarily caused by the plastic growth. Rapid growth gives more and larger eggs and, consequently, better survival in the next generation.
7. The ranking of different populations to subspecies and species must be based on biological and morphological facts. The capacity to live sympatrically in the same lake is decisive if two populations shall be considered as two different species. A comparison between two allopatric populations must in most cases be more uncertain, since the subspecific differentiation may mask the slight morphological difference existing between the species. It seems probable that the whitefish species produce hybrids quite often. There is evidence that these hybrids at least in some cases, may be selected against or sterile.

V. References

- BERG, L. S. 1948. The freshwater fishes of U.S.S.R. and the surrounding countries (Russian). Part I. Ed. 4, Moskau.
- DOTTRENS, E. 1950. Le Corégone actuel du Léman, *Rev. Suisse. Zool.* 57: 789—813.

- FREIDENFELT, T. 1933. Untersuchungen über die Coregonen des Wenersees. *Int. Rev. Hydrobiol.* 30: 49—163.
- HUBBS, C. L. and LAURA HUBBS, 1933. The increased growth, predominant maleness, and apparent infertility of hybrid Sunfishes. *Pap. Mich. Acad. Sci. Art and Letters* 17: 613—641.
- LAURA HUBBS and R. E. JOHNSON, 1943. Hybridization in nature between species of Catostomid fishes. *Contrib. Lab. Vert. Zool. Ann Arbor* 22: 1—76.
- and K. LAGLER, 1947. Fishes of Great lakes region. The Cranbrook Press. Michigan.
- JÄRVI, T. H. 1940. Ueber den Maränenbestand im Pyhäjärvi. *Acta Zool. Fennica* 28: 1—86.
- KOELZ, W. 1931. The Coregonid fishes of northeastern America. *Pap. Mich. Acad. Sci. Art and Letters* 13: 303—432.
- KREITMANN, L. 1929. L'acclimatation du lavaret du Bourget dans le lac Léman et sa relation avec la systématique des corégones. *Actes IVe Congrès intern. Limn.*: 415—433.
- MOTTLEY, MC. C. 1934. The effect of temperature during development on the number of scales in the Kamloops Trout, *Salmo kamloops*, Jordan. *Contrib. Canad. Biol. Fish. N. S. (Ser. A)* 8: 255—263.
- NÜSSLIN, O. 1882. Beiträge zur Kenntnis der Coregonus-Arten des Bodensees und einiger anderer nahegelegenen nordalpiner Seen. *Zool. Anz.* 5: 86—306.
- OTTERSTÖM, C. V. 1922. Helting (*Coregonus albula* L.) og helt (*Coregonus lavaretus* L.) i Danmark. *Undersøgelser af de Ferske Vandets Fiskeriforhold* 2: 1—50.
- SURBECK, G. 1921. Beitrag zur Kenntnis der schweizerischen Coregonen. *Schweizerische Fischerei-Zeitung* 29: 52—59.
- SVÄRDSON, G. 1945. Chromosome studies on Salmonidae. *Rept. Inst. Freshwater Res. Drottningholm* 23: 1—151.
- 1949. The Coregonid Problem. I. Some general aspects of the problem. *Rept. Inst. Freshwater Res. Drottningholm* 29: 89—101.
- 1950. The Coregonid Problem. II. Morphology of two Coregonid species in different environments. *Rept. Inst. Freshwater Res. Drottningholm* 31: 151—162.
- 1951. The Coregonid Problem. III. Whitefish from the Baltic, successfully introduced into fresh waters in the north of Sweden. *Rept. Inst. Freshwater Res. Drottningholm* 32: 79—125.
- THIENEMAN, A. 1912. Die Silberfelchen des Laacher Sees. *Zool. Jahrb. Abt. f. Syst.* 32: 173—220.
- 1915. Untersuchungen an Coregonen. *Zeitschr. Fischerei N. F.* 1: 168—196.
- 1950. Verbreitungsgeschichte der Süßwassertierwelt Europas. *Die Binnengewässer* 18: 1—809.
- TOOTS, H. 1949. Maränenfischerei im Fluss Gimån (Jämtland). *Rept. Inst. Freshwater Res. Drottningholm* 29: 146—152.
- WAGLER, E. 1927. Felchenaufzucht am Bodensee. *Schweizerische Fischerei-Zeitung* 35: 117—121.
- 1937. Die Coregonen in den Seen des Voralpengebietes. IX. Die Systematik der Voralpencoregonen. *Int. Rev. Hydrobiol.* 35: 345—446.
- 1951. Die Felchen (Coregonen) des Laacher Sees. *Zool. Anz.* 147: 18—187.
- VEDEL TÅNING, Å. 1952. Experimental study of meristic characters in fishes. *Biol. Rev.* 27: 169—193.
- WIDEGREN, H. 1863. Bidrag till kännedom om Sveriges Salmonider. *Översigt af Vetenskaps-Akad. Förhandlingar (1863)*: 1—78.
- WIESE, A. 1938. Die Grossmaränen Ostpreussens. *Zeitschr. Fischerei* 35: 475—539.

Reports from the Institute of Freshwater Research, Drottningholm

- *1933. *Gunnar Alm*. Statens undersöknings- och försöksanstalt för sötvattensfisket. Dess tillkomst, utrustning och verksamhet. English summary. No 1. Pris kr. 0:75.
1934. *Gunnar Alm*. Vätterns röding, Fiskeribiologiska undersökningar. Deutsche Zusammenfassung. No 2. Pris kr. 0:75.
- *1934. *Christian Hessle*. Märkningsförsök med gädda i Östergötlands skärgård åren 1928 och 1930. English summary. No 3. Pris kr. 0:50.
1935. *Gottfrid Arvidsson*. Märkning av laxöring i Vättern. Deutsche Zusammenfassung. No 4. Pris kr. 0:75.
- *1935. *Sten Vallin*. Cellulosafabrikerna och fisket. Experimentella undersökningar. Deutsche Zusammenfassung. No 5. Pris kr. 0:75.
1935. *Gunnar Alm*. Plötsliga temperaturväxlingars inverkan på fiskar. Deutsche Zusammenfassung. No 6. Pris kr. 0:75.
1935. *Christian Hessle*. Gotlands havslaxöring. English summary. No 7. Pris kr. 0:75.
1935. *Orvar Nybelin*. Untersuchungen über den bei Fischen krankheitsregenden Spaltpilz *Vibrio Anguillarum*. No 8. Pris kr. 1:25.
1936. *Orvar Nybelin*. Untersuchungen über die Ursache der in Schweden gegenwärtig vorkommenden Krebspest. No 9. Pris kr. 0:75.
1936. *E. Rennerfelt*. Untersuchungen über die Entwicklung und Biologie des Krebspestpilzes *Aphanomyces astaci*. No 10. Pris kr. 0:75.
1936. *Gunnar Alm*. Huvudresultaten av fiskeribokföringsverksamheten. Deutsche Zusammenfassung. No 11. Pris kr. 1:—.
1936. *Gunnar Alm*. Industriens fiskeavgifter och deras användning. No 12. Pris kr. 1:50.
1937. *H. Bergström* och *Sten Vallin*. Vattenförorening genom avloppsvattnet från sulfatcellulosafabriker. No 13. Pris kr. 0:75.
1937. *Gunnar Alm*. Laxynglets tillväxt i tråg och dammar. English summary. No 14. Pris kr. 0:75.
1939. *Gunnar Alm*. Undersökningar över tillväxt m.m. hos olika laxöringformer. English summary. No 15. Pris kr. 2:50.
1939. *Lars Brundin*. Resultaten av under perioden 1917—1935 gjorda fisikinplanteringar i svenska sjöar. Deutsche Zusammenfassung. No 16. Pris kr. 1:—.
1940. *Nils Törnquist*. Märkning av vänerlax. English summary. No 17. Pris kr. 1:—.
1940. *Sven Runnström*. Vänerlaxens ålder och tillväxt. English summary. No 18. Pris kr. 1:—.
1942. *Arne Lindroth*. Undersökningar över befruktnings- och utvecklingsförhållanden hos lax (*Salmo salar*). Deutsche Zusammenfassung. No 19. Pris kr. 0:75.
- *1942. *Lars Brundin*. Zur Limnologie jemtländischer Seen. No 20. Pris kr. 2:—.
1943. *Gunnar Svärdson*. Studien über den Zusammenhang zwischen Geschlechtsreife und Wachstum bei *Lebistes*. No 21. Pris kr. 1:—.
1943. *Gunnar Alm*. Befruktningförsök med laxungar samt laxens biologi före utvandringen. (Fertilization-Experiments with Salmon-parr.) English summary. No 22. Pris kr. 1:50.
1945. *Gunnar Svärdson*. Chromosome Studies on Salmonidae. No 23. Pris kr. 3:—.
1946. *Arne Lindroth*. Zur Biologie der Befruchtung und Entwicklung beim Hecht. (Gäddans befruktnings- och utvecklingsbiologi samt gäddkläckning i glas.) No 24. Pris kr. 3:—.
1946. *Gunnar Alm*. Reasons for the occurrence of stunted fish populations. (Uppkomsten av småväxta fiskbestånd, spec. hos abborre.) No 25. Pris kr. 3:—.
1947. *Gösta Högström*. Olika impregneringsämnenas lämplighet för grovgarnig fiskredskap. Deutsche Zusammenfassung. No 26. Pris kr. 1:—.
1947. *A. Määr*. Über die Aalwanderung im Baltischen Meer auf Grund der Wanderaalmarkierungsversuche im finnischen und livischen Meerbusen i. d. J. 1937—1939. No 27. Pris kr. 2:—.
1947. *Elias Dahr*. Biologiska studier över siken vid mellansvenska östersjökusten. English summary. No 28. Pris kr. 2:—.
1949. Annual Report for the Year 1948 and Short Papers. No 29. Pris kr 3:50.
1949. *Lars Brundin*. Chironomiden und andere Bodentiere des südschwedischen Urgebirgseen. English summary. No 30. Pris kr. 15:00.
1950. Annual Report for the Year 1949 and Short Papers. No 31. Pris kr. 3:50.
1951. Annual Report for the Year 1950 and Short Papers. No 32. Pris kr. 4:50.
1952. Annual Report for the Year 1951 and Short Papers. No 33. Pris kr. 8:—.

* Out of print.

