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INSTITUTE OF FRESHWATER RESEARCH, DROTTHINGHOLM

REPORT No 32

FISHERY BOARD OF SWEDEN

ANNUAL REPORT

FOR THE YEAR 1950

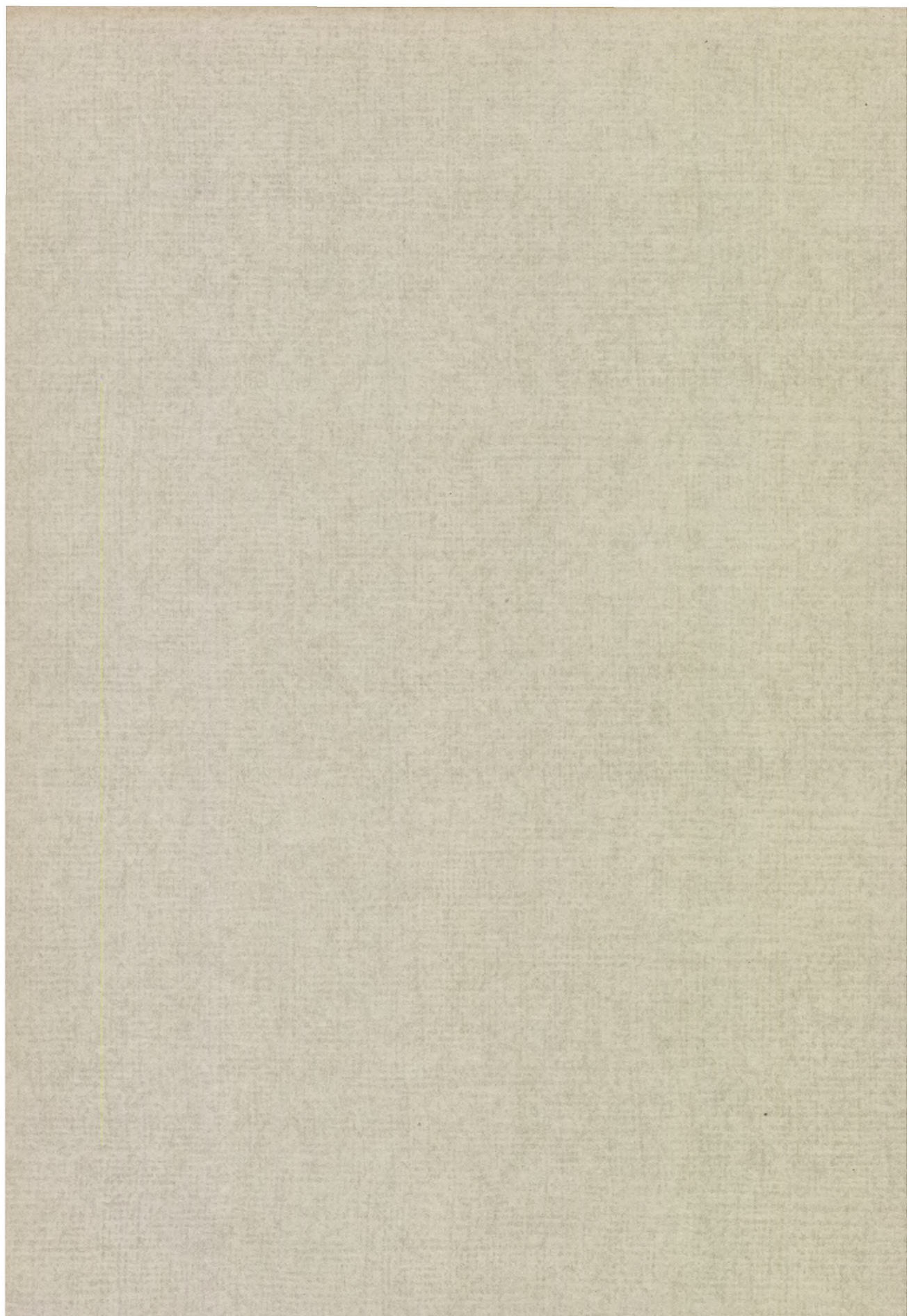
AND

SHORT PAPERS



LUND 1951

CARL BLOMS BOKTRYCKERI A.-B.



INSTITUTE OF FRESHWATER RESEARCH, DROTTHINGHOLM

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Director's Report for the Year 1950

By SVEN RUNNSTRÖM

Members of the Staff in Jan. 1951

Director:	SVEN RUNNSTRÖM, fil. dr.
Fishery Biologists:	LARS BRUNDIN, fil. dr. GUNNAR SVÄRDSON, fil. dr. THOROLF LINDSTRÖM, fil. dr. ERIC FABRICIUS, fil. mag. K.-J. 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 SANDGREN RUTH LARSSON
Laboratory Assistants:	INGRID JOHANNISSON HELVE TOOTS
Porter:	HENNING JOHANSON
Kälarne Research Station (in the Province of Jämtland)	
Fishery Assistant:	E. HALVARSSON

Fil. dr. GUNNAR ALM, who is free from his service as Chief of the Bureau of Freshwater Fisheries, has retained his office at the Institute. HANS RUNNSTRÖM and NILS OLOF ÖSTERBERG have served as extra laboratory assistants. The Migratory Fish Committee (Chairman: fil. dr. G. ALM, Fishery Biologist: fil. dr. B. CARLIN, Assistant: dr. V. MIEZIS, Fishery Assistant: K. B. JOHANSSON, and Laboratory Assistant: ANNA HÄGGLUND) had its office at the Institute last year.

Scientific and Practical Work by the Staff

Studies of the Bottom and Plankton Fauna

BRUNDIN has carried on his investigations of the bottom fauna and its ecology in Swedish oligotrophic lakes. The most extensive fieldwork was done in Katterjaure, an arctic lake in the north of Lappland near Abisko. Katterjaure has an area of 200 hectares and a depth of more than 55 m, an unusually high figure for an arctic lake in Northern Scandinavia. The transparency is low — only about 3 metres — owing to the considerable supply of mud to the lake. The stratification is stable. At the beginning of August 1950 the metalimnion was lying at a depth of about 15 metres. At that time the temperature of the bottom water was 4.2° C. At the shores the temperature of the surface water reached a maximum of 17°, which is probably an extreme figure for the lake. Katterjaure becomes free from ice in July and generally freezes over about October 1. The vegetation is reduced to a belt of *Nitella* at a depth of 4—8 m. Above 4 metres the bottom is sterile and consists of stones and boulders. The bottom of the deep area consists of a light gyttja very poor in coarse detritus. Trout is the only species of fish in the lake.

Test series with a bottom sampler of the Ekman-Birge type disclosed that the bottom fauna has a sharply marked maximum at 4 metres: an average of 3,800 animals per square metre. The predominant group are chironomid larvae of the subfamily *Orthocladinae*. *Pisidium* and *Oligochaeta* are also comparatively numerous. At a depth of 7—10 metres there were about 2,000 animals per sq.m. At greater depths the number of animals decreases further. At 12 metres there were about 1,000, at 17 metres about 800, and at 25—50 metres only about 400 animals per sq.m. In the deeper regions the prominent species of animals are *Heterotrissocladius subpilosus* (*Chironomidae*), *Pisidium conventus*, and *Tubifex* sp.

The experiments with funnel-traps gave surprisingly good results in Katterjaure. They showed, among other things, that during the peak of hatching at the beginning of August no less than about 75 chironomids are hatched every 24 hours per sq.m. at a depth of 4 metres. A total of 45 species of *Chironomidae* were proved to exist in Katterjaure, the greatest number of species known from any arctic lake.

The composition of the bottom fauna and its conditions of existence were further investigated in a number of lakes in the south and middle of Sweden, above all in the deep lakes Ivösjön (Skåne) and Sommen (Östergötland).

STUBE has pursued the investigations in Borgasjön of the fauna living on the bottom vegetation and its importance as food for the trout fry and has been occupied in working up the material.

LINDSTRÖM's studies of the zooplankton production in some lakes in Jämtland were continued last year.

Testing the effectiveness of Artificial Propagation

Pike: SVÄRDSON's studies of the stock of pike in the waters of the Institute in Mälaren and the effect of the planting of pike young marked by fin-cutting were carried on as in earlier years. In the spring of 1950 the spawning fishing began on March 30; during the spawning 252 pike were caught, and after the spawning, up to the spawning season of 1951, a total of 19. The increased yields of the spawning fishing, as compared to earlier years, was probably due to the fact that the water level was higher than during the preceding years. The summer and autumn fishing was inconsiderable in 1951 owing to lack of time.

In Halmsjön, the experimental fishing area of the Institute, the spawning fishing of 1950 began on April 4 and the number of fish caught was 126. After the spawning, up to the spawning fishing of 1951, another 110 pike were caught.

The catches of pike which have not yet been worked up, now comprise the following fishing seasons and yields:

Locality	Beginning of catch year	Number of fish caught:		Total	
		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
Halmsjön	1949—50	April 6	80	292	372
	1950—51	» 4	126	110	236

Thus, it seems clear that the decrease in fishing on spawning pike at Drottningholm in 1948 and 1949 was not due to over-fishing but to other causes.

The fin-cut and planted pike fingerlings have been recaptured to a much larger extent than expected. This marking method has turned out to be so successful that we may expect to acquire some insight into the recruitment of the population, the profitableness of planting pike fingerlings, and the correctness of scale interpretations (»control scales»).

The following recaptures have been made so far:

Marking	Number	Recaptured		
		1948—49	1949—50	1950—51
July 15—17, 1947	274	1	5	9
June 16—22, 1948	699	—	2	6

All the fin-cut pike recaptured have been very easy to identify. Fin-cut fingerlings were planted in Halmsjön, too, in 1949 and 1950, but none of these have been recaptured so far.

In the regional pike investigation, comprising the collecting of statistics from 15 fishermen from various lakes throughout the country as well as alternating plantings of pike fry in the lakes, 5,136 scale samples were gathered during 1950, the total number of pike caught since 1946, when the investigation started, being 23,403.

The colour mutants of pike have lived on, but no new generation has been obtained as yet. Pike seem to have difficulties in getting mature to spawn when they hibernate in aquaria, and it is only when they are transferred into ponds that they can ripe.

Char. ALM has continued the collecting of fishery statistics and scale samples from Vättern with a view to establishing the sizes 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 in 1950 the yields were about 70,000 kg as compared to an average of 59,000 kg for the years 1945—49. Thus, there is no decrease in the yields for 1950 in spite of the fact that the earlier planting that year could affect the stock of fish only to a small degree.

Since 1940 large-scale plantings of char fry have been made in Torrön. From 1945 the plantings have, however, been made only every second year. As RUNNSTRÖM shows in another place in the present report, year-class 1945 has turned out to be very rich, in spite of its having received no support by planting of fry. It is interesting to note that year-class 1945 was predominant in the case of other species of fish and other lakes too. Thus, it would seem that the plantings of fry are of secondary importance for the size of the population compared to other, probably climatic, factors.

Control of Fish Populations.

Salmon: By continued compilation of age-analyses and statistic material from the salmon catches in the Baltic and its most important salmon rivers ALM has established that rich year-classes still exist and that the age-distribution in the catches is, roughly, normal with a predominance of the five- and six-year old salmon, although at the same time in the sea the catches of small salmon under 3 kg has increased during the last few years. The quantity of such salmon delivered to Gotland was as much as 30 % in the spring of 1950, in the autumn of 1949 it was about 19 %, and in the year 1948 about 11 % of the total catches. ALM gave a brief account of the above results at the meeting of the Salmon Committee of the International Council in Copenhagen in October, 1950.

Trout: With a view to obtaining material for a detailed study of the trout population in Storsjön (province of Jämtland) K.-J. GUSTAFSON studied, during the period June 15 to October 15, 1950, the spawning run in Dammån, the most important spawning river for this trout. A fish ladder placed at a

power-generating plant in the lower part of the river served as a trap, and here the length, weight, sex, and number of the trout were controlled. Scale samples were examined for the study of age and growth. In order to get an idea of the intensity of fishing, migrations, and spawning conditions, 864 fish were marked. A preliminary account of these experiments will be found elsewhere in the present report.

RUNNSTRÖM's study of the trout migrations in the fish ladder at Rensjön, was carried on also during 1950.

Char: At the weir in the river Blåsjöälven (Jämtland) 4,778 spawning char (2,635 ♂♂, 2,143 ♀♀) were controlled last year during their migration up the river. Out of these, 1,200 fish were marked.

Grayling: GUSTAFSON's studies of the spawning run of the grayling in the brook Svartbäcken (Storsjön, Jämtland) were continued during 1950, too, and the investigation now comprises also Hegledbäcken, situated 2 kilometres north of Svartbäcken. Out of the 102 fish caught in Hegledbäcken, 7 were marked in Svartbäcken in 1949. When samples were taken at random in another brook, situated 5 kilometres south of Svartbäcken, the ten fish examined included a grayling marked in Svartbäcken the year before. Thus, it would seem that the brook-spawning grayling of Storsjön is not strictly bound to the very same spawning brook. The experience from the markings seems to indicate that up to 90 % of the grayling spawn every year. The down-migration of small fry about 2—3 weeks old, established in 1949, was subjected to a closer examination. During the period June 7—23, 1950, about 45,000 grayling fry left the brook, i.e. 13 % of the spawn laid. During the period September—October 918 fry were caught while emigrating to the lake, but a strong washing away of fry probably occurred at the end of July when the water level was extraordinarily high and temporarily put the trap out of order.

Whitefish: TOOT's investigations of the whitefish spawning run at »Vaktfisket» in the Gimån were carried on. The good fishing during 1948 and 1949, due to the rich year-class of 1945, is now declining and the catches in the autumn of 1950 were less than half of those of the previous year.

In the lake Nälidsjön there is a small-sized species of whitefish, which runs up to spawn in the river Nästån, where large numbers of them are caught in nets. In spite of this intense fishing, the growth of the whitefish has not improved. In the autumn of 1950 a weir was arranged in the Nästån, where all fish running up were to be studied. According to the investigations made there by A. JOHANSON, the catches in the nets consisted almost entirely of males, whereas in the weir males and females were caught in equal proportions. The aim was to let only a small number of fish pass on to the spawning places in order to establish whether this reduction of the fish population might improve the growth of the fish. Unfortunately the weir did not function during the entire spawning period on account of the water level being too high, but the studies will continue with a new weir.

Studies of Factors which Release Fish Spawning

In the Annual Report for the year 1949 FABRICIUS gave a preliminary account of his investigations of the heterogeneous stimulus summation in the release of spawning activities in fish. These investigations were continued during 1950, chiefly as field work and along the following lines.

Pike: The investigations in Vojmsjön in the spring of 1949 proved that a high temperature and the existence of vegetation (*Equisetum*, *Carex*, *Salix*, etc.) were two stimuli that obviously co-operated summatively in the release of the spawning. In the spring of 1950 the water level in Vojmsjön was very low, and so the vegetation zone was reached more than a week later than the previous year; consequently the spawning of the pike did not begin until that time although the warming-up of the water had not been retarded.

Whitefish: FABRICIUS showed that the whitefish spawns to different times in different places in Vojmsjön and that this could be explained by the temperature conditions in the different parts of the lake in relation to the date of freezing over. In 1950 detailed recording of the temperature was started in a number of sections in the lake, thus making it possible to illustrate with figures the advance of the cooling in different parts of the lake during autumn and winter. These observations have confirmed that the spawning of the whitefish occurs at a certain temperature and that the divergences in spawning time are due to the fact that this temperature is reached at different times at different places. Marked whitefish females have also been transferred to another lake, Skikkisjaure, where the whitefish spawn considerably later. The experiment may elucidate the question whether the spawning time is due to temperature and other factors of environment, if any of the marked fish are recaptured later on when spawning.

Char: In Storsjouten, in the autumns of 1948 and 1949, after the lake had been dammed up, a migration of spawning char began up some brooks where spawning had not occurred before. During 1950 the lake was not dammed up, and so the water level was normal during the spawning season in the autumn. It was then established that the char spawned only on the old spawning grounds in the lake, and did not migrate up into the brooks. Thus, the migration during the two damming-up periods of 1948 and 1949 had not created a lasting habit, but was only the direct result of the situation during the damming-up periods.

Speciation of Fish

Whitefish: SVÄRDSON continued his investigations, collecting a considerable number of new whitefish samples from lakes all over the country and from the Baltic Coast during 1950. By employing a special assistant, which was made possible by a grant from Statens Naturvetenskapliga Forskningsråd

(the National Science Research Council), the routine work, such as measuring, counting gillrakers etc., could be done faster during the winter of 1950—51. Several thousands of whitefish were examined and SVÄRDSON devoted the greater part of the year to the study of the rich material. A third paper in the series »The Coregonid Problem» has been written and will be found elsewhere in this Annual Report. It is still somewhat uncertain whether there are four or five different species of whitefish in this country, but the recent investigations lend further support to the view that the whitefish belong to different species.

Trout: The investigations carried out by ALM at Kälärne of different forms of trout are being pursued. They show the previously mentioned differences in colouration and in the sexual maturity of small-sized trout and their offspring, and also that the sexual maturity is reached earlier by populations with a better growth, and that the good growth persists in spite of spawning. It would seem that the offspring of the river trout spawn every year but that this is not the case with the Vätter trout, at least not to the same extent. The experiments also aim at finding out the length of life of the fish. In the autumn of 1950 there were 7 river trout F2, 13 years old, 11 of the same form, 11 years old, and 6 Vätter trout, 11 years old, also in F2.

Hybrids: During 1950 ALM continued the hybridization experiments with salmon ♀×sea trout ♂, and sea trout ♀×salmon ♂. During the winter of 1949—1950 the experiments were repeated at the fish-culture stations of Mörrum and Älvkarleö. The results were varied and in some cases the hybridization experiments and the control experiments showed no great divergences. Hybrids are still kept at Kälärne. Thus, in the autumn of 1950 there were 550 two-summer-old fishes of salmon ♀×sea trout ♂ with a length of 8—21 cm, and 450 two-summer-old fishes of sea trout ♀×salmon ♂, length 8.5—17 cm. The fry resulting from the 1949—50 experiments were kept in troughs at the fish-culture station of Kvarnbäcken. The mortality in series of great and small number of fry was considerably greater among the hybrid than among the control fry.

The experiments to rear a second generation from bastards of char ♀×brook trout ♂ have yielded very poor results. However, in the autumn of 1950 there were at Kälärne a small number of two-summer-old specimens, 7.5—12 cm long, and 450 one-summer-old specimens, 4—10 cm long. The offspring of (char×brook trout) ♀×brook trout ♂ has proved more satisfactory in so far as there were 114 two-summer-olds 9—19 cm long, and 500 one-summer-olds, 4.5—9 cm long.

Perch: During 1950 ALM's studies at Kälärne of the relation between sexual maturity and growth both in single individuals and in different populations of perch chiefly aimed at producing slowly growing and fast growing populations by modifying the density of population and by using

ponds more or less rich in food. In the autumn of 1950 there were in various ponds the following number of specimens: 1) 650, length 6—9.5 cm, 2) 650, length 7—9.5 cm, 3) 130, length 8—11 cm, 4) 89, length 10.5—12.5 cm, and 5) 45, length 10—14 cm.

The experiments aim at finding out if the percentage of the number of sexually mature fish in the spring of 1951 is different in the different populations, and the relative size of the sexually mature and not mature fish in each population.

As regards earlier experiments with perch it may be mentioned that in the autumn of 1950 there were left 6 small-sized perch transferred to a pond in the spring of 1934, now 28—38 cm long, and consequently more than 20 years old (17 years in a pond and transferred when 4—5 years old). There were, too, 14 perch 16 years old and 25—34 cm long, reared from the beginning in ponds. The experiments will be carried on with a view to establishing the length of life and increase in growth. All the ♂♂ and ♀♀, in both experiments spawn every year.

Studies in Regulated Lakes

In a paper in the present Report RUNNSTRÖM gives an account of 14 years' observations in a lake regulated for the production of electric power, Torrön, where especially the char population has been studied. Contrary to what has been supposed before, the fluctuations in the water level of the lake have not greatly affected the renewal of the population, in spite of the fact that great quantities of spawn are destroyed when the water level is low in the winter. On the other hand, a considerable decrease in the growth rate has occurred, so that the average weight of the char has greatly declined. This is probably due to the fact that the food production of the lake has decreased and it is evidently necessary to concentrate the future investigations on the conditions of food production in the regulated lakes.

Practical Studies of Fishing Gear

Impregnation Experiments. A comprehensive experiment begun by MOLIN in 1949 was brought to an end in 1950. Besides substances suitable for only coarser tackle, most substances that may be used in the impregnation of snaring tackle were also included. — A fresh impregnation experiment was begun in the summer of 1950 with a view to establishing the impregnating qualities of some new substances. At the same time experiments were begun in some different types of lakes in order to find out the difference in rotting. In these experiments one substance from each of the groups tannin, copper, and tar, was represented.

Nylon Experiments. MOLIN's earlier studies of the suitability of nylon

thread for the manufacture of fishing tackle were continued. Threads of different types and manufactures were subjected to various tests, and test fishing was performed with the ready-made tackle.

Publications in the Year 1950

The following papers by the staff of the Institute and other members of the Fishery Board have been published during the year:

Rep = Report from this Institute.

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

ALM, G. Preliminary report of certain experiments with a view to exploiting lakes empty of fish. *Rep.* 31: 19—25.

— The seatrout-population in the Åva stream. *Rep.* 31: 26—56.

— Storleken och användningen av enl. 2 kap. 10 § vattenlagen utdömda fiskeavgifter. *SFT.* 59: 5—7.

— Nyare fiskeribiologiska rön och deras tillämpning i praktiken. *Hushållningssällskapens tidskrift.* 3—4: 70—74.

— Fiskens ålder och tillväxt. *Sportfiskaren* 16: 75—77.

— Laxfiskarena och 1940-talets goda laxår. *Ostkusten* 1: 6—7.

— Fiskodling. En fiskevårdsåtgärd både på gott och ont. »*Fisken vid disken*». *Svängsta.* Årg. 2, 1: 4—6.

— Kronans fiskevatten och deras utnyttjande. »*Napp och nytt från Svängsta*», *bihang till Sportfiskaren.* 6: 18—23.

CARLIN, B. Några intryck från en studieresa till Storbritannien och Irland. *SFT.* 59: 68—71.

DAHR, E., Kräftpesten 1950. *SFT* 59: 148.

FABRICIUS, E. Heterogeneous stimulus summation in the release of spawning activities in fish. *Rep.* 31: 57—99.

— Något om instinkthandlingarnas medfödda utlösningmekanism. *Svensk Faunistisk Revy* 12: 83—94.

— Varför är den ena flugan bättre än den andra? *SFT* 59: 179—183.

GUSTAFSON, K. J. Harren i Storsjön. *SFT* 59: 82—84.

JOHANSON, A. The white-fish population of Lake Ocke. *Rep.* 31: 100—109.

LINDROTH, A. Reactions of crayfish on low oxygen pressure. *Rep* 31: 110—112.

— Laxbeståndens fluktuationer i de norrländska älvarna. *Sv. vattenkraftföreningens publ.* 415 (1950: 5): 103—224.

— Fiskeriintressets kamp mot vattenförorening i England. *Vattenhygien* 6 (4): 95—100.

LINDSTRÖM, T. Kvantitativa studier av kräftdjursplankton i några jämtlandssjöar. *SFT* 59: 57.

— Lake Trout och fiskutsättningens lönsamhet. *SFT* 59: 163—165.

MOLIN, G. The fitness of nylon thread for manufacture of fishing tackle. *Rep* 31: 113—118.

— Result of impregnation experiments. *Rep* 31: 119—126.

— Nylontrådens användbarhet för tillverkning av fiskredskap. *SFT* 59: 42—45.

MÄÄR, A. A supplement to the fertility of char (*Salmo alpinus* L.) in the Faxälven water-system, Sweden. *Rep* 31: 127—136.

— and RUNNSTRÖM, S. *Lepidurus arcticus*, PALLAS in Indalsälven and Faxälven water-systems, Sweden and Norway. *Rep* 31: 147—150.

PUKE, C., The possibility of avoiding winter-kill of fish. *Rep* 31: 137—146.

RUNNSTRÖM, S. Director's report for the year 1949. *Rep* 31: 5—18.

— Sillens mysterium löses? *SFT* 59: 53—54.

- and MÄÄR, A. *Lepidurus arcticus* PALLAS in Indalsälven and Faxälven watersystems, Sweden and Norway. *Rep 31: 147—150.*
- SVÄRDSON, G. The Coregonid problem II. Morphology of two Coregonid species in different environments. *Rep 31: 151—162.*
- Vad bestämmer fiskars lektid och lekplats? *SFT 59: 8—12.*
- SÖRENSEN, I. Ueber biologische Reinigung phenolhaltiger Abwässer. *Kungl. Fysiogr. Sällsk. Förhandl. Bd 20. Nr 9: 1—10.*
- VALLIN, S. Sockerbrukens avloppsvattenfrågor, kampanjen 1949. *Socketmeddel. 6: 285—290.*
- Planktonpest utanför medelpadkusten. *SFT 59: 122—125.*
- Gästriklands Storsjö och industrin. *Natur i Gästrikland: 228—236.*

The Tagging of Char, (*Salmo alpinus*, LINNÉ) in Lake Vättern

By GUNNAR ALM

Introduction

In the deep and cold water of Lake Vättern a stock of char has survived since the period after the Ice Age. Char is the most important fish in the lake, the average yield being some 60,000 kg a year.

The char reach a considerable size: the mean weight varying from 0.4 kg to 1.5 kg, corresponding to a length of about 38—50 cm. Yet char weighing as much as 4 and 5 kg, and measuring some 70—80 cm in length, have been caught. The age of the fish of average weight is 5—7 years (ALM 1934).

During the years 1919—1943 all char fishing was forbidden in the lake at spawning time, normally from October 5th to November 20th. A number of fishermen were, however, granted permission to catch char for the purpose of collecting eggs for the hatcheries on the lake, in particular for the large hatchery at Borensult, near the town of Motala. Since 1944 there has been no artificial hatching or output of char. Autumn fishing has been forbidden only at the spawning grounds, which are situated at places where there are big rocks and stones at a depth of 1—10 m. The char have, therefore, been allowed to spawn undisturbed. In the near future we should be able to compare the results of the year classes spawned naturally with those of the preceding years, spawned partly artificially and partly naturally. In a few years time the char in this lake will all be naturally spawned, and then I hope to be able to reach a final decision in this matter.

For the purpose of gathering information as to the migration of the char and the intensity of the fishing in the lake, the fish were tagged as early as in the thirties. This tagging material has not yet been subjected to a thorough study: I have, however, compiled the results, as they must be of importance in the questions mentioned above.

Tagging Methods and Places

The taggings were carried out by the supervisor of the Borensult Hatchery, sometimes by the fishermen themselves. Tagging was started in 1933, using

Table 1. Number of tagged and recaptured char (percentages of recapture in brackets).

Year of tagging	Number tagged			Number and percentage of recapture		
	♂♂	♀♀	Total	♂♂	♀♀	Total
1935	142	121	263	66 (46,5)	62 (51,2)	128 (48,4)
1936	126	171	297	43 (34,1)	61 (35,7)	104 (35,1)
1937	92	106	200 ¹	48 (52,2)	46 (43,4)	95 (47,5) ³
1938	74	123	199 ¹	32 (43,2)	42 (34,1)	74 (37,2)
Total	434	521	959 ²	189 (43,6)	211 (40,5)	401 (41,8) ³

¹ Sex not recorded for 2 fish.² » » » » 4 »³ » » » » 1 »

Table 2. Number of char tagged at different places, and number and percentages (in brackets) of recaptured specimens.

Tagging place and tagging years	Number tagged			Number and percentage of recapture		
	♂♂	♀♀	Total	♂♂	♀♀	Total
I. Västanvik 1935—37	41	36	77	24 (58,5)	21 (58,3)	45 (58,4)
II. Erkarna—Fjuk 1936	20	12	32	14 (70,0)	5 (41,7)	19 (59,2)
III. Höjern—Rödesund 1935—36	65	55	120	38 (58,5)	25 (45,5)	63 (52,5)
IV. Borghamn 1935—38	56	61	117	22 (39,3)	28 (45,9)	50 (42,7)
V. Flisen 1937—38	23	19	42	13 (56,5)	8 (42,1)	21 (50,0)
VI. Björknäs—Hjo 1935—38	104	199	306 ¹	24 (23,1)	73 (36,7)	98 (32,0) ²
VII. Stava 1935—37	48	27	75	28 (58,3)	12 (44,4)	40 (53,3)
VIII. Visingsö 1935—38	77	112	190 ²	26 (33,8)	39 (34,8)	65 (34,2)
Total	434	521	959 ³	189 (43,6)	211 (40,5)	401 (41,8) ²

¹ Sex not recorded for 3 fish.² » » » » 1 »³ » » » » 4 »

only fine silver threads attached to the adipose fin. In all 108 specimens, 70 males and 38 females, were tagged. In 1934, 138 — of both sexes — were tagged, the threads being attached to the dorsal fin. Finally, in 1935, 30 males and 21 females were tagged, the silver threads being attached to the caudal fin. All these taggings were carried out on spawning fish caught during October and November at the spawning grounds at Höjern (Fig. 1).

Table 3. Number and percentages of char in different length groups caught by different methods of fishing.

	Length in cm											
	26-30	31-35	36-40	41-45	46-50	51-55	56-60	61-65	66-70	71-75	76-80	Total
Troll fishing												
1924—33	23	110	134	281	149	66	27	15	1	—	—	806
0/0	2,8	13,6	16,6	34,5	18,5	8,2	3,3	1,9	0,1	—	—	
1946—50	—	39	1.485	1.739	1.059	520	201	80	38	6	—	5.167
0/0	—	0,7	28,7	33,6	20,5	10,1	3,9	1,5	0,7	0,1	—	
Spawning fishing												
1924—33	—	1	28	63	73	55	59	38	14	3	1	335
0/0	—	0,3	8,3	18,8	21,8	16,4	17,6	11,3	4,2	0,9	0,3	
Tagged 1935—38 ¹	—	4	51	84	170	255	216	119	46	3	—	948
0/0	—	0,4	5,4	8,9	17,9	26,9	22,8	12,5	4,8	0,3	—	

¹ No particulars about the length of 11 sp.

In 1935 numbered plates were used in tagging; this method was also employed during the years 1936—38. The tags consisted of numbered silver plates attached by means of fine silver threads. They were affixed either in front of, or behind, the dorsal fin. The following figures show that the greater part of the recaptures consisted of fish bearing the tag in front of the dorsal fin. 475 fish were tagged in front of the dorsal fin, of which 214, or 45.1 % were recaptured. The corresponding figures for fish bearing the tags behind the dorsal fin were 384, 145 and 37.8 %. In several cases we have no information as to the position of the tags.

The recaptures also show that, in many cases, the tags had been in position for several years, in some instances up to 6 years from the date of tagging. This kind of tagging, therefore, proved satisfactory.

Tagging operations were concentrated to the spawning grounds and spawning season, October and November. In this way only spawning fish were tagged. The tagging places, altogether 8 in number, are situated in different parts of the lake, see Fig. 1. They are marked in italics. 959 char were tagged with numbered plates (Tables 1 and 2). At tagging places VI and VIII females were in the great majority, and at I, II, V and VII males were predominant.

The length of the tagged and non-tagged spawning fish is shown in Table 3: this table also gives the length of non-spawning char caught at other seasons. From these figures it is evident that the size of the tagged char has been considerable, slightly larger than the normal size of spawning char, and far larger than that of char caught in other seasons and at places other than the spawning grounds. It will also be seen that the normal size of char caught in recent years is about the same as it was in the thirties.

Tagging Results

Number of Recaptures

Of the 1933 taggings, when the tags consisted only of silver threads, as many as 17 males (24.3 %) and 8 females (21.1 %) were recaptured. The results of the thread-taggings of 1934 and 1935 were not so good, only 3 (2.2 %) and 2 (3.9 %) were recaptured.

Tables 1 and 2 give the numbers of recaptures in the different tagging years and at the various tagging places. Altogether 401, or 41.8 %, were recaptured. The results of the different tagging years (Table 1) vary between 35.1 % and 48.4 %, the figures for the tagging places show even greater variation (32 % and 59.2 %). The smallest recaptures were made at the places where the greatest number of fish were tagged (VI and VIII), and the best recaptures at those places where the smallest number had been tagged (II). This would suggest that, during comprehensive tagging, the same care may not have been taken as at minor taggings. However, at VI and VIII the taggings were spread out over the whole period of 4 years, so that the number tagged each year cannot have been so great. The conclusion cannot, therefore, be correct. Another factor which might influence the results is the percentage of males and females at the various taggings, as the recaptures show considerable variations at different places. But this offers no explanation, as the percentage of male and female recaptures varies greatly.

It might perhaps be possible that the size of the char tagged has some bearing on the results of the recaptures. If natural mortality is greater among the bigger and older fish than among the smaller and younger ones, one would expect fewer recaptures from those length groups. Thus, if mainly smaller char were tagged at one place, and larger at another, the results of the recaptures must be different. However, it will be seen in Table 4 that the percentage of recaptures is only a little smaller in the larger length groups. Further, specimens of both length groups were tagged at all the tagging places. Finally, I would like to mention the fact that at tagging places VI and VIII the tags were often affixed behind the dorsal fin, a method said to be less satisfactory than the forward position. However, the differences in recaptures may be due to causes still unknown.

Places and Dates of Recapture (The Migrations of the Char)

The dates and positions of catches of tagged char reported by fishermen may not always be quite accurate. In many cases no information has been offered when returning the tags. But on the whole they give a good idea of the occurrence and migrations of the char in the lake at different seasons.

Table 4. Number of tagged and recaptured char in different length groups.

Number of individuals	Length when tagged in cm								
	31—35	36—40	41—45	46—50	51—55	56—60	61—65	66—70	71—75
Tagged	4	51	84	170	255	216	119	46	3
Recaptured	—	24	40	64	115	76	49	25	1
Percentage recaptured}	0	47,0	47,7	30,8	46,7	35,1	41,1	54,3	33,3

I give the results of the eight different taggings on separate maps (Figs. 2—9), the key will be found on Page 26.

Fig. 1, mentioned above, shows all the recaptures during the months of January—September and December, the part of the year when there is no spawning. During this period the char are to be found in all parts of the lake, though more rarely in the extreme northern and southern ends. At spawning time, as I have already pointed out, no fishing has been allowed outside the spawning grounds.

If we turn now to Figs. 2—9, we see that the fish tagged at the most northerly tagging places (in particular I and II) were almost always recaptured in the northern parts of the lake, only a few recaptures from these taggings have been made elsewhere. This is also applicable in some measure to the recaptures from tagging places III and V. In the same way, though not to the same degree, most recaptures from the southern tagging places VII and VIII were made in the southern and central parts of the lake. Further, recaptures from the intermediate tagging place VI have been made in all parts of the lake.

This may be due, to some extent, to the fact that the recaptures of the northern taggings, in particular of I and II, consisted mainly of spawning fish which had returned to their earlier spawning grounds (i.e. tagging places). But it may also indicate that the char in the lake belong to different stocks, which mostly occur in different parts of the lake.

The maps, however, also show that the char often migrate to different parts of the lake, and that the recapturing places vary considerably at different seasons. Very soon after tagging several specimens have migrated a good distance and have been caught in other parts of the lake. Some recaptures from the taggings at I had moved 30 km, at II 20 km, at V 20 km and 60 km, at VI a large number had migrated 20 km and one 40 km, at VII 30 and 40 km, and at VIII several specimens were found 30—50 km away from the tagging places. But a number of char remained for some time at the tagging places and were recaptured there (I, III, IV and, in particular, VIII). Recaptures outside the spawning months of October and November were made mainly at points 20—30 km from the tagging places, though some were made at a distance of 40, 50 and 60 km. However, a large

Table 5. Total number of recaptured char in different seasons and in different years after tagging.

Years of recapture	Seasons for recapture								Total ¹			
	Jan.—March.		Apr.—June		July—Sept.		Oct.—Dec.		♂♂	♀♀	Total	‰
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀				
Tagging year ...	—	—	—	—	—	—	21	21	24	25	49	12,8
First year.....	18	13	22	20	29	25	49	37	133	103	236	61,8
Second year.....	2	9	5	9	7	10	5	15	22	43	65	17,1
Third year	—	1	—	4	1	7	—	4	1	18	19	5,0
Fourth year.....	—	—	—	2	—	4	2	1	2	7	9	2,3
Fifth year	—	—	—	—	1	1	—	1	1	2	3	0,8
Sixth year	—	—	—	1	—	—	—	—	—	1	1	0,3
Total	20	23	27	36	38	47	77	79	183	199	382	
	43		63		85		156		6 ²	12 ²	19 ²	
	(12,4 ‰)		(18,1 ‰)		(24,5 ‰)		(44,9 ‰)		189	211	401	

¹ In these figures are also included specimens about which information with regard to season is lacking.

² Specimen of which neither season nor year is known, sex not recorded for one fish.

number of fish were recaptured within the areas containing the tagging places. Further, the maps show us that recaptures during the spawning season are concentrated to special parts of the lake, the spawning grounds. Thus the interesting fact emerges that these recaptures have, in the main, (67.6 ‰ of all the fish caught during the spawning season) been made at the respective tagging places. The fish have, therefore, returned to their earlier spawning grounds to spawn again. The majority (77.5 ‰) of these home-spawning fish have returned to spawn and been caught the following year, but a large number have not been caught until the second, some in the third and one in the fifth year.

The 34 tagged fish recaptured in the autumn at other spawning grounds have, with few exceptions (some sp. in taggings III, V and VII) not migrated to spawning grounds at any great distance. And the majority, or 82.4 ‰, of the spawning fish caught at other grounds have returned after only one year. Therefore, these results indicate that the majority of the char spawn at least two, and more probably several, years in succession.

Let us now turn back to the maps and consider the dates of recapture. The maps give us the seasons and years in which the recaptures were made. The corresponding figures for the whole material will be found in Table 5. We see that the largest recaptures were made in the last three months of the year, 45 ‰ of all recaptures. A considerable number were also made during July—September. The smallest number of recaptures occur during the first months of the year (12.4 ‰). These figures are partly dependent

Table 6. Number and percentages of recaptures in the spawning-season (Oct.—Nov.) in relation to all recaptures where season is known.

Recapture	Tagging place								Total
	I	II	III	IV	V	VI	VII	VIII	
Total	32	17	53	16	40	89	36	60	343
Oct.—Nov. ...	17	8	20	6	15	21	7	11	105
%	53,1	47,1	37,7	37,5	37,5	23,6	19,4	18,3	30,6

on fishing intensity. Fishing is generally at its peak in the later summer months, decreasing on account of the ice in the winter months. The fact that the fish are concentrated at the spawning grounds in the autumn, and therefore easy to catch, may account for the numerous recaptures during the autumn months. However, the relation of recapture to season is very different at the tagging places, as will be seen in Table 6 and the maps. More than 53 % of all recaptures from tagging place I were made during the spawning months. In fact, an unusually large number of returns were not accompanied by information as to the time of recapture, but they were probably caught during the spawning season. Another tagging place, No. II, has also yielded a large number of returns during the spawning months (47.1 %). On the other hand, the tagging places at the southern end of the lake (VII and VIII) show only a few spawning returns (19.4 and 18.3 % respectively). This may be explained in part by the fact that in all probability fishing at the spawning grounds at the northern end of the lake was intensive in the thirties and forties, for the purpose of collecting eggs for the hatcheries, as mentioned above. This does not apply in the same degree to the southern parts of the lake and, therefore, a relatively large number of recaptures from the southern tagging places must have been made at other seasons.

Table 5 also shows that in the whole material the most numerous recaptures (61.8 %) were made in the year following the tagging year, though a considerable number of fish were recaptured in the second and third years, and some as late as the fifth and sixth year after the date of tagging. Some recaptures (12.8 %) were made later in the tagging year.

Now I would like to draw attention to a rather interesting point. Table 7 shows several cases in which fish, caught and tagged at the same place and on the same day, were recaptured at about the same date, in some cases on the same day, months or years after being tagged. This applies both to fish recaptured at the spawning grounds in the autumn and recaptures made at other seasons. Recaptures have been made, for instance, in the summer two and four years after tagging. This fact indicates quite clearly that the char school together and, if nothing occurs to separate them, probably remain in the same school all their lives. In some cases these fish belong to the same sex, in others both sexes have been represented.

Table 7. Char tagged and released at the same place and the same date, and recaptured together later on.

Tagging place	Tagged			Recaptured		
	Date	Sex	Length in cm	Date	Length in cm	Position
I	26/10 36	♂	44	26/10 37	45	I
	»	♀	55	»	57	I
II	3/11 36	♂	54	21/10 37	56	II
	»	♀	44	25/10 »	52	II
	»	♀	62	27/10 »	66	II
III	22/10 36	♂	64	27/11 37	64	III
	»	♀	61	29/10 »	63	III
	29/10 35	♂	48	20/7 39	56	Axstål (near Åsen)III)
	»	♀	55	8/8 »	56	
IV	3/11 38	♂	52	18/10 39	56	IV
	»	♀	59	19/10 »	62	IV
	27/10 35	♂	34	16/10 36	37	VIII
	»	♀	46	19/10 »	56	VIII
VI	2/11 35	♂	59	4/11 36	64	Fågelås (near Fågelås)VI)
	»	♀	?	5/11 »	?	
	5/11 36	♂	53	17/11 37	60	N. Visingsö
	»	♀	56	»	59	N. Visingsö
	»	♂	54	29/10 37	55	V
	»	♀	56	»	57	V
	»	♂	41	5/11 »	42	VI
	»	♀	55	6/11 »	57	VI
	3/11 37	♂	65	2/11 38	65	VI
	»	♀	61	»	64	VI
	7/11 38	♂	66	23/7 39	65	III
»	♀	60	»	60	III	
VIII	7/11 35	♂	57	12/11 36	62	N. Visingsö
	»	♀	57	17/11 »	60	N. Visingsö
	7/11 36	♂	62	25/11 38	62	Jönköping
	»	♀	52	9/12 »	56	Jönköping
	5/11 38	♂	57	11/12 »	58	IV
»	♀	51	18/12 »	55	IV	

What has been said above indicates that the char in different parts of the lake belong to different local populations. These populations are not, of course, separated by either geographical or physiological boundaries. At food migration time they generally mix, though the char in I-population do not, as a rule, go to the southern parts of the lake. In the spawning seasons, too, they sometimes go to different spawning grounds in different years. In the main, however, they seem to return to their earlier spawning grounds. It should also be borne in mind that, owing to differences in water temperature at the northern and southern ends of this large lake, the northern char start spawning earlier than the southern. This may play some part in keeping the populations separate.

Mortality of the Char and Fishing Intensity in Lake Vättern as shown by the Tagging Results

Finally, on the basis of the tagging results, let us study the important question of whether the stock of char in Lake Vättern is adequately exploited or not. First, however, we must discover what effect the tagging may have on the fish.

Earlier tagging experiments in other fish-species have led to a study of this question. As a rule, the tagged fish have shown less satisfactory growth and general condition than intact fish. Although a large number of tagged fish have shown normal growth for their size and age, several have been retarded. It is true, of course, that the information available as to the size of the recaptured fish is often inaccurate and unreliable.

In Table 8 data have been compiled on the increase in length of tagged char recaptured towards the end of the year following tagging, and later. The average increase is also given. The table shows that a number of char have increased only very slightly in length, occasionally not at all, and some show a decrease. This is seen most clearly in the case of the larger specimens, when the recaptures have been made several years after tagging. Other specimens again have shown an increase which compares well with the normal growth of char in Lake Vättern (ALM 1934), some 6—7 cm a year. However, the retarded growth of some specimens has reduced the average to far below the normal growth figures. Bearing in mind the inaccuracy of information received as to length of recaptures, and despite the fact that many specimens have shown normal growth, the results indicate that the general condition of the tagged fish is less satisfactory than that of intact char. Yet, in the majority of cases, the tagging has probably not affected the condition of the char so much that mortality among these fish has been far higher than among the intact fish. Otherwise it would be difficult to account for the numerous recaptures, a large number several years after tagging.

The yield of the char fisheries on Lake Vättern during the period 1936—40 has varied little, the average weight being some 55,000 kg a year. The lake has probably been fished at about the same rate during this period, the stocks of char in the lake being proportionate to the yield. Therefore, one may assume that the relation between the recaptures of tagged char and the occurrence of tagged specimens in the lake is the same in the second and following years as it is in the first year of recapture. Further, the difference between the estimated number of tagged char remaining from one year to another, and the number of occurring tagged char, computed on the basis of the recaptures, may be assumed to give the natural mortality.

In Table 5 we see that in the whole material as many as 49 char were recaptured in the tagging year. Therefore, at the beginning of the following year not more than 910 (959—49) tagged specimens remained in the lake.

Table 8. Growth increment in cm during one or several years in tagged char of different length groups.

Growth increment in cm	Length groups in cm at tagging and number of years before recapture																											
	35—40		41—45			46—50			51—55			56—60			61—65			66—70			71—75							
	1	2	1	2	3	1	2	3	4	5	1	2	3	4	5	1	2	3	1	2	3	1	2					
— 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
— 1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
± 0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
± 1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
18	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
Total number	8	1	15	1	2	20	5	3	1	1	29	8	5	1	1	23	9	2	1	1	11	3	2	12	3	2	9	6
Average growth increment in cm	3,8	14,0	3,5	3,0	12,5	4,6	7,5	7,7	7,0	10,0	3,5	5,0	9,0	1,0	14,0	2,8	4,4	6,0	6,0	9,0	1,5	3,3	6,0	1,4	3,3	6,0	2,9	2,7

Of these, 236 or 25.9 % were recaptured that year. At the end of the year, then, about 670 (910—236) tagged char ought to have been left, if no mortality had occurred. In the second year, however, only 65 recaptures were made. On the basis of the percentage mentioned above, 25.9 %, these 65 recaptures correspond to a tagged stock of 250. The difference, $670 - 250 = 420$ (or ab. 46 % of 910), should represent the mortality in the first year. In the same way one can estimate that, without mortality, the number of tagged specimens at the end of the second year ought to be 185 (250—65). As only 19 char were recaptured in the third year, indicating a remaining stock of 73 tagged specimens, the mortality during the second year should be $185 - 73 = 112$ (or ab. 45 % of 250). The recapture figures for the fourth and fifth years are too low to allow any calculation of the mortality rate.

These figures do, however, indicate a relatively high rate of mortality. But in all probability it is concentrated to the larger and older groups corresponding to the most common size of the tagged char, which is unusually high, rather than to the majority of char caught (Table 3). These char are much smaller and, of course, younger: the figures dropping rapidly for the bigger sizes.

In the main the char are troll-fished, with hook and line. As this gear has no selective influence as regards the size of the fish caught, at least not among the bigger sizes, the figures in the table 3 probably give the real size and age composition of the char stock in the lake. They indicate a rapidly increasing rate of disappearance in the older groups, due to both fishing and natural mortality. If the tagging results could be applied to the intact fish, the figure for mortality would be relatively high when the char reach a length of about 50 cm. But it is also possible that the lake is fished rather heavily, as the high number of recaptures would appear to indicate. However, the question of whether the fishing rate can be said to be too high for the stock of char, cannot be discussed until the problems mentioned in the introduction have been dealt with. Nor can we deal in this paper with the matter of age and size of the fish caught, their size on reaching sexual maturity compared with the number of immature fish caught, or possible means of augmenting the yield.

Summary

During the period 1935—1938, 959 char, of which 434 were males, 521 females and 4 not sexed, all in the length group 35—75 cm., were tagged in Lake Vättern. The char were caught and released at different spawning grounds during the spawning season (October and November). During the following years 189 males and 211 females, a total of 401 (one not sexed) were recaptured, equal to 43.6 %, 40.5 % and 41.8 % respectively. 49 were recaptured in the tagging year, 236 the following year, and 65, 19, 9, 3 and

1 in the second to sixth year after tagging. The char were recaptured in all parts of the lake with the exception of the northern and southern ends in which recaptures were very rare. The results of the various taggings indicate that the char are divided into several distinct populations in different parts of the lake, and that they mostly return to their own grounds to spawn. In a number of cases tagged specimens have been recaptured at the same time, one or two years after being tagged, indicating school adherence between individuals. The figures for recaptures, 26 % during the first year, and the figures for the normal size of the char in the catches as a whole indicate a relatively high rate of natural mortality among the bigger and older groups and perhaps also a comparatively heavy fishing.

Reference

ALM, G. 1934: Vätterns röding, fiskeribiologiska undersökningar. Deutsche Zusammenfassung. *Inst. Freshw. Research. Report 2: 1—26.*

Key to the maps (Fig. 2—9).

In several cases no information has been obtained regarding the year or locality of recapture. These recaptures have not been included on the maps.

The following signs are used:

- Recaptured in the months January—March
- ◉ » » » » April—June
- ⊕ » » » » July—September
- » » » » October—November
- ◉ » » » » December
- » » » » with no information regarding season.

Strokes on the circles indicate years passed after tagging.

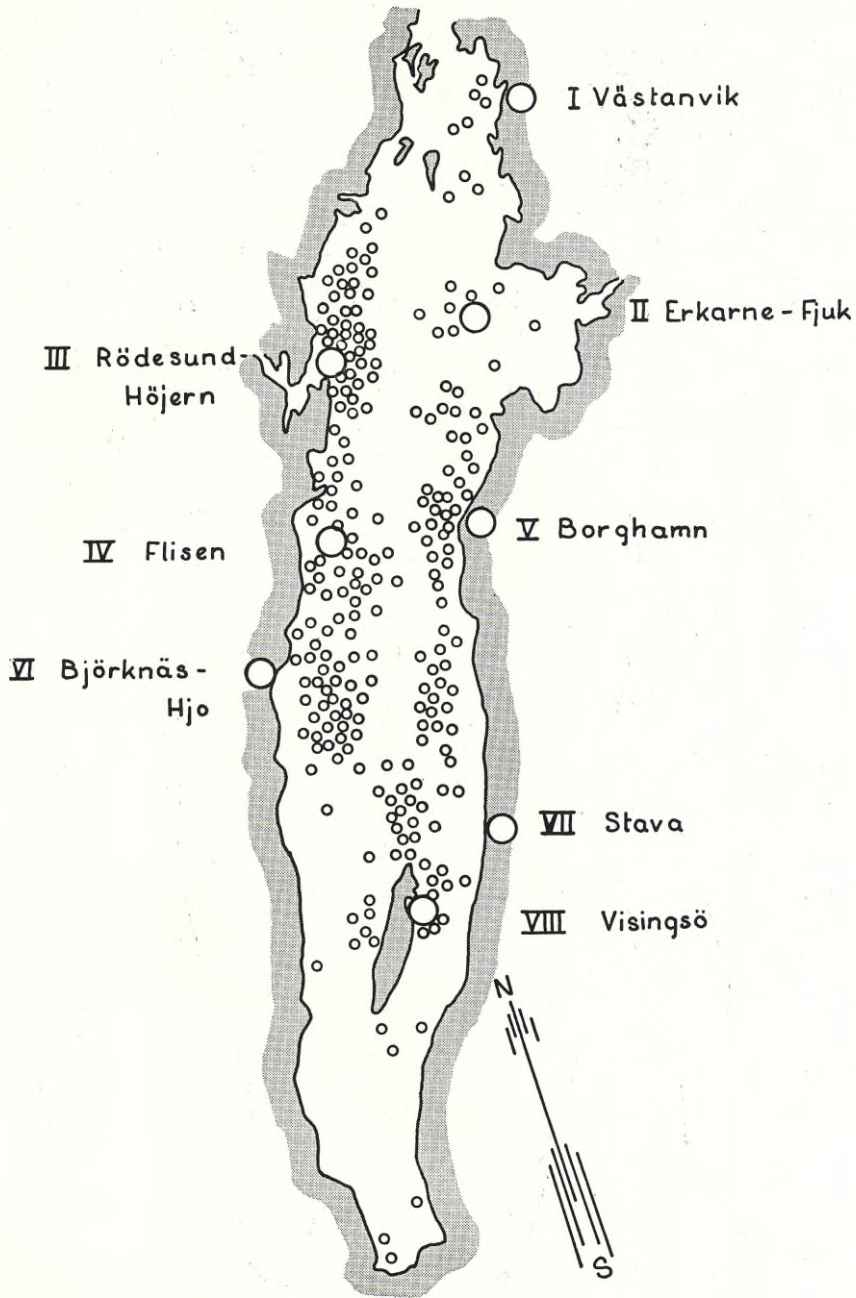


Fig. 1. Tagging places I—VIII and recaptures in the nonspawning months Jan.—Sept. and Dec.



Fig. 2. Recaptured char, tagged at place I. Fig. 3. Recaptured char, tagged at place II.



Fig. 4. Recaptured char, tagged at place III. Fig. 5. Recaptured char, tagged at place IV.



Fig. 6. Recaptured char, tagged at place V. Fig. 7. Recaptured char, tagged at place VI.



Fig. 8. Recaptured char, tagged at place VII. Fig. 9. Recaptured char, tagged at place VIII.

The Relation of O₂-microstratification at the Mud Surface to the Ecology of the Profundal Bottom Fauna

By LARS BRUNDIN

It has long been evident that the concentration of oxygen in the bottom water greatly influences the life conditions and composition of the bottom fauna within the deep areas of lakes. Whereas lakes with a hypolimnion rich in oxygen are characterized by a polyoxybiontic *Tanytarsus* fauna rich in species, lakes with a hypolimnion poor in oxygen show a euryoxybiontic *Chironomus* fauna poor in species. And if the bottom water always lacks oxygen, not even the *Chironomus* fauna can exist. Then, only anaerobic bacteria are left.

In determining the oxygen concentration of the bottom water a comparatively large sampler is generally used, and this is lowered close to the mud surface. As early as 1922, however, ALSTERBERG, basing his view upon convincing tests, pointed out that during a longer or shorter period of the year the hypolimnial bottom water in most lakes undoubtedly displays a distinct so-called microstratification in contact with the mud surface. The mud, which is practically without oxygen, is rich in reducing substances which consume the oxygen store of the bottom water, and the result is that the oxygen concentration drops sharply in the water layers — a few millimetres or centimetres thick — lying immediately over the mud surface. When a sample is taken with an ordinary sampling-vessel the oxygen concentration of a column of water about 15—20 cm high is determined. It is evident that it is not possible to obtain by this method a reliable value of the oxygen concentration of the layers close to the mud surface which represent the respiratory environment of the bottom fauna. The oxygen concentration there is certainly often considerably lower than what is shown by the test. ALSTERBERG's view on the microstratification has been studied further — mainly in its theoretical aspects — by GROTE (1934), and others.

Of course, great technical difficulties are involved in the study, under natural conditions, of the interchange of dissolved substances that takes place between the mud and the bottom water in lakes. A method must be used, by which samples can be taken of the surface mud and the water immediately overlying it, so that the chemical stratification is undisturbed.

A »surface mud sampling apparatus» which satisfies far-reaching requirements in this respect has been used successfully by MORTIMER (1941/42, 1949) in his studies in the Lake District in England. Among other things, MORTIMER has been able to study in detail the redox (oxydation-reduction) gradient, which is confined within the dimensions of a few millimetres near the mud surface. His results show that the redox potential itself controls the distribution of dissolved substances in natural lake systems and that the concentration of oxygen exerts its influence on the system largely through its effect on the potential. As long as the oxygen concentration at the mud surface has not fallen below about 1 mg/l, a surface skin a few mm thick is observed to be different in colour and texture from the underlying mud. By exploring the vertical distribution of the redox potential it can be shown that oxidizing conditions extend only to the base of this surface skin, which is called the »oxidized surface layer» by MORTIMER, and which owes its different appearance to the presence of ferric hydroxide. The lower limit of this layer can approximately be taken as the isovolt $E_7 = 0.20$ V, which in Blelham Tarn (Lake District) corresponds to an oxygen concentration of about 0.5 mg/l. The thickness of the oxidized surface layer reflects a dynamic balance between the oxygen demand of the mud and the oxygen supply maintained by water movements at the mud surface. Decrease in the latter during thermal stratification is followed by a decrease in thickness of the oxidized layer. If the oxygen concentration of the bottom water drops below 1 mg/l, the oxidized surface layer disappears, which implies that the $+0.2$ isovolt moves nearer the mud surface and reaches the free water. In this position the oxygen concentration in the hypolimnion decreases comparatively quickly, and the reduction processes which have previously been confined to the mud, make themselves felt in increasingly higher hypolimnical layers. Ferrous iron appears in the water in increasing concentrations. MORTIMER points out that on account of turbulent diffusion the reduction rate is much higher in the hypolimnion than in the mud, where molecular diffusion alone is operative. The great hypolimnical gradients result in a »macrostratification» in the sense of ALSTERBERG. But the degree of turbulent diffusion is not the same in the hypolimnion of all lakes. MORTIMER shows that this is proportional to depth and area. The diffusion coefficient also varies with the depth in the same lake. This is, in its turn, important considering the available supply of oxygen with which the mud surface is in contact. Here the morphometrical factor becomes operative in a high degree.

ALSTERBERG (1922, p. 21) arrived at the conclusion that a distinct microstratification also exists in typically oligotrophic lakes. On the whole, subsequent studies have confirmed this view. Thus, we may conclude that the oxygen concentration of the hypolimnical bottom water can become a minimum factor for some bottom animals in oligotrophic lakes also, where with the aid of the ordinary water sampler we can establish comparatively

high oxygen values in the bottom water. The hypolimnical bottom areas of the oligotrophic lakes are, however, probably not equivalent as respiratory environments. For, to all appearances, the oxygen-absorbing power of the mud is very low, the thickness of the oxidized mud layer considerable and the microstratification only very slightly indicated in the extremely oligotrophic mountain lakes of Fennoscandia and the Alps. With regard to respiratory conditions, the profundal region of different lakes consequently affords a wide range of environments, with the extremes represented, on one hand, by the pronouncedly eutrophic lakes with protracted macrostratification, and on the other by the extremely oligotrophic lakes with only a slightly indicated microstratification. To this must be added that the oxygen stratification of the bottom water may generally be assumed to be fairly heterogeneously developed on different levels in the profundal region of the same lake.

The question is now how the bottom fauna, and particularly the chironomids, are affected by different profundal respiratory conditions.

Before we try to answer that question, we must, however, first discuss the respiratory biology of the species we are concerned with. The most characteristic animals of eutrophic lakes, the big, lively red larvae of the genus *Chironomus*, are widely known. The striking colour emanates from the red pigment erythrocrucorin, which is closely related to haemoglobin (SVEDBERG and HEDENIUS 1934). The *Chironomus* larvae are typical mud-dwellers, and it has been established by LENZ (1931) and K. BERG (1938) that the larvae of the species *anthracinus* ZETT. (*bathophilus* KIEFF., *Liebeli* KIEFF.) and *plumosus* L. penetrate far down into the oxygen-free mud, frequently 30—40 cm below the mud surface. When the larvae breathe, they sit in their tunnels with their heads closest to the mud surface, and by rhythmical undulatory movements of the body they produce a water current down the tunnel. The current provides them not only with oxygen and — under certain circumstances — food in the form of living and dead plankton but also washes away accumulated carbon dioxide or organic acids. In this connection it is of great interest that LINDROTH (1942) has been able to prove that under favourable respiratory conditions the *Chironomus* larvae display a marked periodicity in their ventilation work! Thus, the ventilation pauses of *C. plumosus* have a duration of 11—21 minutes at 5—7° and 3—5 minutes at 18—19°. According to LINDROTH (1943), the *plumosus* larvae spend their ventilation pauses down in the mud, where they are occupied in feeding and digging. On the other hand, tests (cf. for instance ALSTERBERG, l.c., K. BERG, l.c.) show that with decreasing oxygen concentration the *Chironomus* larvae become increasingly confined to the neighbourhood of the mud surface and that, at the same time, the ventilation work becomes increasingly continuous.¹ When the oxygen pressure is lowered

¹ On the basis of LANG's experiments on *Chironomus plumosus* and *Thummi* larvae in experiment vessels containing strong concentrations of phytoplankton (LANG 1931, p. 96),

somewhat more, the larvae cease feeding and concentrate what energy they can muster on breathing movements. Finally they creep down into the mud, where they can spend many weeks in a more or less markedly anaerobic state (cf BERG 1938). It may be pointed out, however, that the duration of the anaerobic periods under natural conditions may easily be overrated on account of the technical difficulties that are encountered in establishing very small oxygen concentrations. It is often a question of micro-aerobiosis where the existence of anaerobiosis has been assumed (GROTE 1934, p. 112).

The function of the erythrocrucorin of the chironomid larvae is not yet fully elucidated. The results hitherto attained show that the erythrocrucorin functions as an oxygen carrier only at low pressures of oxygen corresponding to about 5—44 % saturation at 17° C. (EWER 1942, WALSHE 1947 a, b).

WALSHE (1947 b), however, has found that this mechanism is far less effective in *Microspectra praecox* MEIG. (*Tanytarsus brunnipes* ZETT.) living in streams than in the *Chironomus* species. She supposes that the presence of erythrocrucorin in the *Tanytarsus* group may perhaps be due to some quality other than its oxygen transporting ability.

According to HARNISCH (1936, etc.), erythrocrucorin plays an important part in supporting the secondary oxybiosis, i.e. the intense respiratory process («Erholungsatmung») that comes into play after a preceding anaerobiosis. Later, however, HARNISCH (1942, 1950 a, b) and WALSHE (1947 a) could show that the secondary oxybiosis cannot be a general phenomenon and that in certain euryoxybiontic species, such as *Chir. anthracinus* and *plumosus*, it is replaced by endoxybiotic processes.

LINDROTH (1943) is of the opinion that HARNISCH has underrated the importance of erythrocrucorin under normal conditions, because he has studied the larvae in artificial environments and made his experiments as purely physiological investigations. An environment which forces the *Chironomus* larvae to spend long periods in anaerobic condition, and retards the completion of the metamorphosis and thus causes considerable mortality, by no means affords optimal life conditions.

As pointed out by LEITCH (1916), the oxygen confined to the erythrocrucorin is sufficient to supply the oxygen demand during about 12 minutes, which is in good agreement with the length of the ventilation pauses (vide above). For that reason LINDROTH (1943) supposes that the erythrocrucorin of the *Chironomus* larvae serves in a transport as well as a storing mechanism, and that in the latter case this substance is of great biological importance as the animals can thereby suspend ventilation for certain periods in order to satisfy their need of food, a function which would probably otherwise be difficult or impossible. That would be in accordance with the conditions found in

we may presume that the nutritive importance of the water current is very great in small eutrophic waters with abundance of plankton — independent of the oxygen concentration of the respiratory environment.

some marine worms. According to LINDROTH this would apply to the *Tubificidae*, too.

In view of the ecology of the larvae and the proved existence of erythrocrucorin in the family *Chironomidae*, LINDROTH's hypothesis seems very probable. For, in so far as the chironomid larvae appear as typical mud inhabitants in the profundal region of lakes, they are with few exceptions (some *Orthocla-diinae*, see below) provided with erythrocrucorin. These red larvae all belong to the subfamily *Chironominae*. They represent quite a considerable number of species, distributed among several genera, the best known of which are: *Chironomus*, *Sergentia*, and *Stictochironomus* of the *Chironomus* group, *Lauterbornia*, *Microspectra*, and *Tanytarsus* of the *Tanytarsus* group.

There are, however, some typical mud dwellers among the chironomids, whose larvae lack erythrocrucorin and are of a white or greenish colour. They are members of the subfamily *Orthocla-diinae*. A characteristic of this systematic group is that the larvae require an environment rich in oxygen, and it is significant that the group is particularly richly represented in running water and in arctic and alpine lakes. In conformity with this, the profundal mud dwellers among the *Orthocla-diinae* are pronouncedly stenotopic forms, which require a high oxygen pressure close to the mud surface. To this group belong, in the first place, *Heterotrissocladius Grimshawi* EDW., *H. Määri* BRUND., *H. subpilosus* KIEFF., *Monodiamesa bathyphila* (KIEFF.) PAG., *M. Ekmani* BRUND., *Protanypus morio* ZETT., and *P. caudatus* EDW., all of which belong to the characteristic species of the oligotrophic or ultraoligotrophic deep fauna.

There are, however, certain gradations in the relations of these species to the oxygen factor. To all appearances, *Monodiamesa bathyphila* and *Protanypus morio* are the least sensitive to unfavourable respiratory conditions. These two species have, however, the biggest larvae (length 14—16 mm), a fact which will probably be of importance in this connection (see below). The larva of *Monodiamesa bathyphila* feeds on living and dead algae and moves slowly, creeping through the mud (LANG 1931, PAGAST 1947), probably only in the surface layers. The larva of *Protanypus morio* is a predator which moves swiftly and seems to feed chiefly on chironomid larvae and *Oligochaeta* (LANG l.c., PAGAST l.c.). Just by their way of living the *Monodiamesa* and *Protanypus* larvae are probably more favoured as far as the microstratification is concerned than are stationary mud inhabitants with corresponding reactions to oxygen pressure.

The same thing applies to some species among the *Orthocla-diinae*, which, among other things, have the characteristic in common that the larvae live in freely mobile tubular houses. Of these species *Heterotanytarsus apicalis* KIEFF., *Microcricotopus bicolor* ZETT., and *Abiskomyia virgo* EDW. are found in harmonic oligotrophic lakes far beyond the vegetation belt of the shores and sometimes at considerable depths. The two first-mentioned species

have been found, in the south of Sweden, even in the profundal region of polyhumic lakes, where microstratification is probably quite pronounced (BRUNDIN 1949). *Abiskomyia*, on the other hand, is only known from arctic-subarctic lakes in the north of Sweden.

To sum up, we can establish that with regard to the erythrocrucorin-free larvae, i.e. the *Orthocladiinae*, as profundal mud inhabitants, they are, unlike larvae with erythrocrucorin, on the whole bound to environments with particularly slightly developed microstratification.

As is well known, chironomid larvae of the genera *Chironomus*, *Sergentia*, *Stictochironomus*, and *Tanytarsus* sens. lat. (*Tanytarsus*, *Lauterbornia*, *Microspectra*) have played an important part in the characterization of different trophic types among lakes. In so far as larvae of these genera are predominant in the profundal fauna of the lakes they are taken to indicate a scale from eutrophy to oligotrophy in the order mentioned. Then must be added as indicators of extreme oligotrophy some members of the subfamily *Orthocladiinae* (in Fennoscandia especially *Heterotrissocladius subpilosus*, BRUNDIN 1949). The value of the above-mentioned chironomids as trophic indicators is limited, however, as their behaviour is without doubt more directly determined by the oxygen factor; and there is no binding connection between trophic standard and O₂-stratification in hypolimnion.

But when it can be proved that the larvae of *Chironomus plumosus*, *Chir. anthracinus*, *Sergentia coracina*, *Stictochironomus Rosenschöldi*, *Tanytarsus lugens*, and *Heterotrissocladius* represent a series of species with increasing sensitiveness to unfavourable respiratory conditions, we may well seek the reason for this. It seems rather natural that the *Heterotrissocladius* larvae are most sensitive, as they lack erythrocrucorin. It is, however, not so clear why the other types, all of which are provided with that red colour stuff, should differ from each other.

The careful experiments carried out by WALSHE (1947 b, 1948) on the larvae of *Microspectra praecox* show that the metabolic rate in this species is dependent on the oxygen pressure in the water at all pressures below that corresponding to air saturation. The oxygen consumption is high in fully aerated water (higher than in *Chironomus* larvae) and falls with declining oxygen pressure. In normal *Chironomus* larvae from stagnant water the oxygen uptake at 17° C. is constant and independent of the oxygen concentration of the water down to about 15 % air saturation (EWER 1942, WALSHE 1947 b). Unfortunately WALSHE has not studied larvae of the *Tanytarsus* group from profundal lake bottoms. Perhaps their adaption for life in these environments has resulted in lower metabolic rates than those of the *Tanytarsus* larvae from running water?

Experiments hitherto carried out indicate, however, that the effectivity of the respiratory mechanisms is very divergent in different chironomid larvae. At low oxygen pressures the effectivity is higher in the *Chironomus*

than in the *Microspectra* larvae, and this in spite of the fact that the volume of the body in relation to the surface is much smaller in *Microspectra*. The relatively great body surface of *Tanytarsus* (*Microspectra*) again causes greater losses of heat than in *Chironomus*, which implies a higher metabolic rate in *Tanytarsus*.

HARNISCH (1950 a) is of the opinion that the lower metabolic rate of euryoxybiontic chironomid larvae under favourable respiratory conditions is due to the constant activity of endoxybiotic processes in these larvae.

These physiological characteristics, however, may only partly explain the different resistance of red chironomid larvae to O₂-microstratification in lakes. To all appearances, another factor of great importance is the size of the larvae.

ALSTERBERG (1922, pp. 67—72, fig. 16) has shown that the *Tubificidae* pump water down from higher water layers by undulating movements of the free posterior part of their bodies, and that, at decreasing oxygen pressure, these animals work with larger and larger parts of their bodies in order to increase the effect. He points out that the water current is in direct proportion to the area of the body that is active. This applies to the chironomid larvae, too, but they are handicapped in so far as they in general perform their respiratory movements below the level of the mud surface.

The ability of different chironomid larvae to pump down water from higher water layers is no doubt very varied. Thanks to their size and greater muscular power the *Chironomus* larvae must achieve a far greater effect than the small *Tanytarsus* larvae. Moreover the capillary force proves a greater obstacle in the thin *Tanytarsus*-tubes. The following table indicates the body proportions of some chironomid larvae (final instar) which are of special interest in this connection:

	Length mm	Width mm	Body surface: 2 mm ²
<i>Chironomus plumosus</i>	28.0	2.0	87.9
<i>Chironomus anthracinus</i>	18.0	1.35	38.5
<i>Sergentia coracina</i>	14.0	0.80	17.6
<i>Stictochironomus Rosenschöldi</i>	11.5	0.74	13.3
<i>Tanytarsus</i> sp. (medium size)	7.0	0.5	5.5

We see that the part of the body that is active in the rhythmic undulating movements (i.e. about half of the body surface) is in *Stictochironomus Rosenschöldi* about 2 ¹/₂ times, in *Sergentia coracina* about 3 times, in *Chironomus anthracinus* about 7 times, and in *Chironomus plumosus* no less than 16 times larger than in *Tanytarsus*. It is important to note that the order in which the larvae are grouped in the table, represents a series with decreasing body size and that this order directly corresponds to the proved ability of the

larvae to manage under unfavorable respiratory conditions! This can hardly be an accident.

With regard to the microstratification the size of the larvae must be very important. A *Chironomus* larva affects water layers situated far higher over the mud surface than those affected by the little *Tanytarsus* larva. The critical height of the respiratory layer is much lower for a *Tanytarsus* larva than for a *Chironomus* larva. Consequently *Tanytarsus*, under similar circumstances, reaches a critical situation far earlier than *Chironomus*, even on the presumption that the effectivity of the respiratory mechanisms is accordant.

It was pointed out above that the O_2 -concentration of the hypolimnial bottom water can probably constitute a minimum factor for some bottom animals in oligotrophic lakes, too. The facts and conclusions produced by ALSTERBERG, MORTIMER and others seem to indicate that even in such lakes the distance of the respiratory layer from the mud surface can, more or less temporarily, become too great for, for instance, small chironomid larvae of the *Tanytarsus* type. If we consider, too, that the development of microstratification varies with the depth, there is reason to suppose that the bottom fauna within the profundal region of oligotrophic lakes should display at least a trace of a zonation conditioned by the O_2 -microstratification. This seems, moreover, to be the case. Of interest within the harmonic-oligotrophic type of lakes are particularly shallow, moderately oligotrophic lakes with inconsiderable hypolimnion, in Sweden for instance Innaren and Skären in Småland and Västra Skälsjön in Västmanland (cf BRUNDIN 1949).

In Lake Innaren, which is 19 m deep, the white larvae of *Heterotrissocladus Grimshawi* show a pronounced abundance maximum at a depth of 8—9 m (upper profundal), whereas at greater depths they occur very sparsely in spite of seemingly favourable oxygen conditions. The lower profundal of Innaren is completely dominated by red *Tanytarsus gregarius* larvae.

In Lake Skären, which is 27 m deep, the maximum of abundance in September 1943 occurred for *Heterotrissocladus Määri* at 13—16 m, for *Microspectra insignilobus* and *Tanytarsus* at 16—24 m, for *Stictochironomus Rosenschöldi* at 26—27 m. (Only stray *Sergentia coracina* larvae were found at 20 and 24 m.)

In Västra Skälsjön, which is 19 m deep, the maximum of abundance in August—September 1943 occurred for *Tanytarsus* at 10—13 m, for *Stictochironomus Rosenschöldi* at 13—16 m, and for *Sergentia coracina* at 18 m. *Heterotrissocladus Määri* larvae were found in August at a depth of 10—18 m, most of them at 18 m, but there was no trace of them in profundal in September — after the hatching. As the hatching begins in shallower water and then moves to deeper water, it is probable that the bathymetrical distribution of the *H. Määri* larvae in August did not give a true picture and that the maximum of abundance during the greater part of the year occurs at higher levels.

In these lakes we can, with the aid of a water sampler, establish a certain decrease in the oxygen concentration of the bottom water towards the end of the stagnation periods, which indicates far-reaching changes in the microstratification. On September 9 1943, in Lake Skären, the oxygen concentration at the greatest depth was 2.91 mg/l (temperature 10.0°); on September 29 1943, in Västra Skälsjön, the oxygen concentration at the greatest depth was 4.09 mg/l (temperature 9.7°). These oxygen values do not imply any sub-minimal oxygen pressures for the bottom animals, but they obviously indicate the existence of a microstratification which is comparatively unfavourable for small chironomid larvae of, for instance, the *Tanytarsus* group, but which hardly affects the bigger *Stictochironomus* and *Sergentia* larvae. Therefore it seems probable that the bathymetrical distribution of the chironomid larvae in the profundal of Skären and Västra Skälsjön shows, at least to some extent, the connection between the size of the larvae and the concentration of erythrocyruorin on the one hand, and the development of the O₂-microstratification on the other.

In this connection it must, however, be pointed out that the bathymetrical distribution of the chironomid larvae is quite reversed in very deep oligotrophic lakes, for instance Bodensee, Walensee, Briener See, and Thuner See in the Alps, and in Vättern in the south of Sweden. Studies by LUNDBECK and others reveal that in lakes of this type the *Stictochironomus* and *Sergentia* larvae reach their maximum at quite a moderate depth. At greater depths there is a zone with a predominance of *Tanytarsus* (*Microspectra*) larvae and, furthest down, a zone where the *Orthoclaadiinae* larvae reign almost supreme. LUNDBECK (1936) points out that this zonation is doubtless due to the fact that, in lakes of this type, the food supply gradually decreases towards the depth. The remains of plankton coming from epilimnion are largely dissolved before they reach the deepest profundal regions where, too, the sedimentation of litorigenous material is extremely slight. In this extremely oligotrophic environment the O₂-microstratification is no doubt very slight, a condition to the advantage of most *Orthoclaadiinae* larvae.

In view of the development of the O₂-microstratification and the height of the respiratory layer above the profundal mud surface, we will probably be justified in distinguishing two main types among the oligotrophic lakes:

1. The shallow Skären type with a cup-shaped basin, where the O₂-microstratification is more clearly marked and the height of the respiratory layer above the mud surface increases with growing depth.
2. The deep Bodensee type with a trough-shaped basin, where the generically slight O₂-microstratification and the height of the respiratory layer remain fairly constant or are weakened and decreased with increasing depth.

In discussing the possible connection between the size of the chironomid larvae and their varying power of resistance to O₂-microstratification, the

question also arises how the new-hatched larvae of the profundal species behave. It should then be observed that the size of the new-hatched larvae is in proportion to that of the final instar larvae. The new-hatched larva of the genus *Tanytarsus* is little more than 0.5 mm long, that of *Chironomus anthracinus* 1.5 mm long (THIENEMANN 1922, p. 615). Thus, the latter should be able to neutralize O₂-microstratification more easily than the former. But on the other hand, the new-hatched *C. anthracinus* larva is considerably smaller than a final instar larva of *Tanytarsus*.

Without doubt the first stage of the larva is always a critical period in the cycle of metamorphosis. A study of the phenology shows, however, that the profundal *Chironomidae* species treated here swarm and spawn in more or less direct connection with the spring and autumn circulations of the lakes when the O₂-microstratification is entirely eliminated. The first stage of the larva therefore generally encounters favourable conditions in the profundal of eutrophic lakes, too.

It has only been my aim here to touch upon some aspects of the relation of bottom organisms, and particularly the chironomids, to the oxygen factor. The anaerobiosis presents special and very intricate problems, and in concluding I only desire to stress the interesting studies of SSINITZA (1937) on the relation between the redox potential of the chironomid larvae, the concentration of erythrocrucorin and the ability of the larvae to stand anaerobiosis. SSINITZA reaches the astonishing result that larvae without erythrocrucorin in this respect display greater tolerance than those provided with that colour stuff. Among the erythrocrucorin-free larvae (*Psectrotanypus*, *Culicoides*) the redox processes take place more slowly than in *Chironomus*, and during anaerobiosis the comparatively high redox potential remains almost constant, whereas in *Chironomus* it is relatively low in oxygen environments and decreases greatly during anaerobiosis.

It should be observed, however, that SSINITZA's studies of erythrocrucorin-free larvae only comprise free-living predators of the family *Ceratopogonidae* and the subfamily *Tanypodinae* among the *Chironomidae*. It seems extremely improbable that his result should apply also to the erythrocrucorin-free larvae of the subfamily *Orthoclaadiinae*.

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The Topography of the Spawning Bottom as a Factor influencing the Size of the Territory in some Species of Fish

By ERIC FABRICIUS

1. Introduction

Territorial behaviour during spawning is known in several species of fish belonging to many different systematic groups. I may here refer to an introduction given by NOBLE (1938). In these species of fish every male, or spawning couple, choose a small territory within which no other sexually active fish of the same species are tolerated, thereby limiting the number of couples within a certain area. From a fishery-biological point of view, the size of the spawning territory is of particular interest, for the size of the separate spawning territories indirectly decides how much spawn may be laid on a bottom area of a given size.

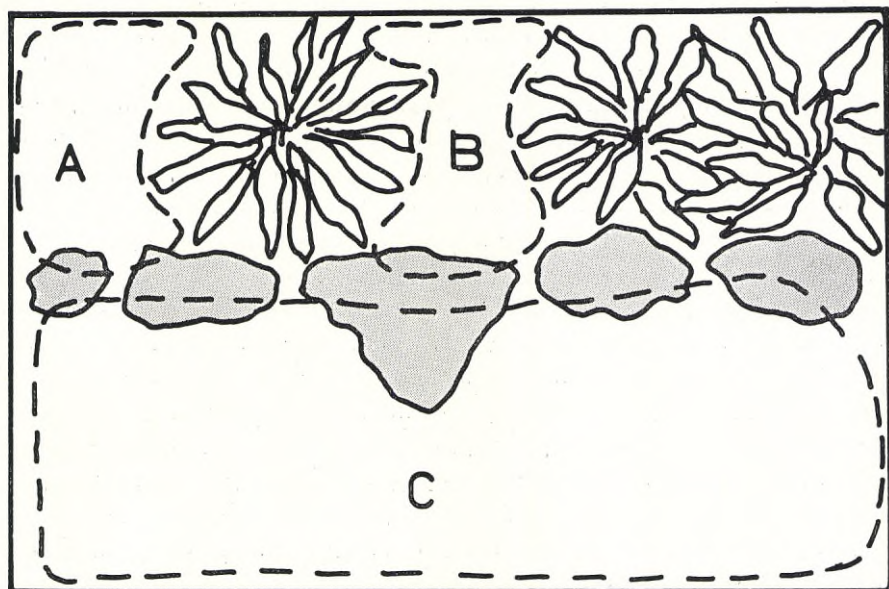
As has been pointed out by, for instance, BREDER (1934), the territorial behaviour of fish resembles closely that of birds, which has been the subject of detailed study for many years. I need only refer to the compilation of the literature on the territorial behaviour of birds made by ARMSTRONG (1947, p. 271 pp.). The size of the territories of birds is first determined by the distance within which the territory-guarding bird may attack intruding competitors. HOCHBAUM (1944), who has studied these phenomena with regard to ducks in particular, says that the boundaries of territory are the boundaries of the drake's tolerance. This »distance of tolerance» is, however, not constant but to a large extent elastic, for in a sparsely inhabited area, the territories are generally considerably larger than in an area which is densely inhabited. Thus, HUXLEY (1933) has very aptly compared the territories of birds to elastic discs, of which there is a lower as well as a higher number which can be placed together to cover a given area, and, as several authors have pointed out, this also applies to the territories of fish (cf. for instance, BAERENDS & BAERENDS 1950). The individual variation in body-size is of course much greater in fish than in birds, thus it is possible to investigate if the »distance of tolerance» of the territory-guarding fish is influenced by his own body-size. In fact, this has been done by BREDER (1936) and BAERENDS & BAERENDS (op.cit.), who established that large fish as a rule have considerably

larger territories than small individuals. In addition to the »distance of tolerance» characteristic of every species of fish, the density of population and the individual size of the fish, the size of the territories is also influenced by other factors, as will be illustrated below by a few examples.

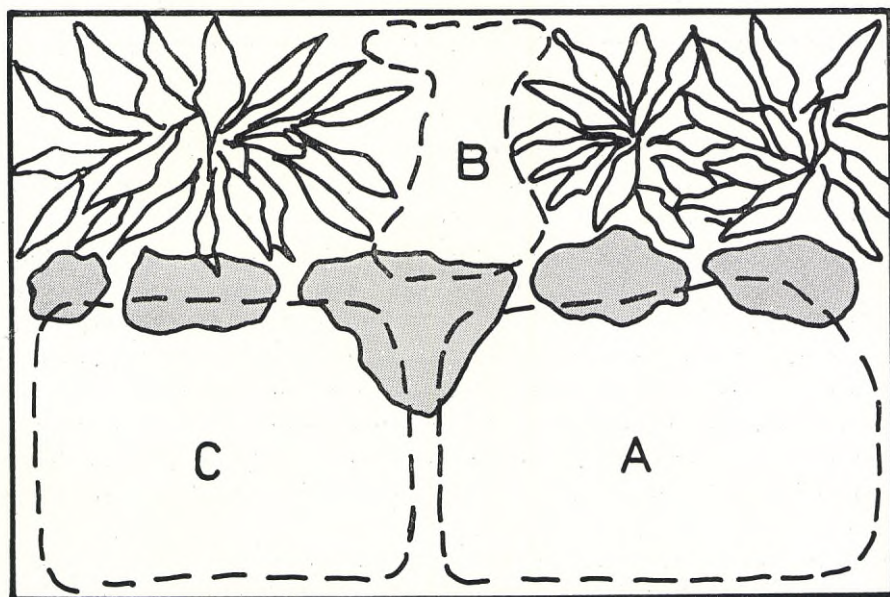
2. The Spawning Territories of *Tanichthys albonubes*

For several years I have studied, in aquaria, the spawning habits of the small Chinese fish *Tanichthys albonubes* belonging to the family *Cyprinidae*; the aquarium-keeper's »red tail» or »white cloud mountain fish». In spawning the males of this species have proved to be strongly territorial. Every male chooses a small territory on the bottom, within which he stays the whole time, and if there are several males in one aquarium their territories border on each other. Now and then one of the males makes a sudden advance into the territory of one of his neighbours. The holder of the territory immediately swims towards him, and both fish show a very marked lateral display (TINBERGEN 1948). They stand side by side, not parallel to each other but with their tails nearer to one another than their heads, so that the length axis of one fish forms an angle of about 30° with that of the other. The dorsal, caudal, anal, and ventral fins expand, so that the beautiful red edging of the fins is displayed, the red-edged pectoral fins flap quickly and rhythmically in a strange »mark time», and the whole fish trembles in a characteristic manner. After standing like this for a few moments, the two antagonists dart away in opposite directions with a sudden jerk. It very seldom comes to a real fight, but one or two such demonstrations of lateral display suffice, as a rule, to make the intruder flee and return to his own territory. If an intruder does not respond with a lateral display when the territory-guarding male approaches, the latter does not show any lateral display either, but attacks immediately and violently. This is noticeable especially when they drive away females that are not quite ready to spawn and which have invaded the territory. The females, too, can show lateral display against each other, and I have even seen females defending territories, thereby exhibiting typically male behaviour with both lateral display and attacks.

From January to May, 1950, I kept three males and two females of *Tanichthys albonubes* in an aquarium, the bottom area of which was 22×35 cm. By keeping the temperature at $+20^\circ$ Centigrade I could keep the fish sexually active the whole time, each of the males constantly defended his territory, and the fish spawned time and again with only a few days' interval. The three males were individually recognizable on account of small differences in the shape of some of their fins. It soon became clear that their territories were very different in size (Fig. 1 a). The largest territory, held by the male C, stretched along the whole front of the aquarium, which was free from plants, whereas the males A and B each had much smaller



a) January—March.



b) April—May.

Fig. 1. The territories of three *Tanichthys* males (A, B, C) in an aquarium. Spring 1950.

territories between groups of plants at the back of the aquarium, where the vegetation was dense. In this case there was no positive correlation between the body-size of the males and the size of the territories. On the contrary, the largest and obviously most powerful of the males, B, had the smallest territory, which consisted of only a glade, hardly more than 5 cm broad, between two thick groups of *Cryptocoryne* plants, whereas the smallest fish, C, had the largest territory. Fish A had his territory between a group of plants and the glass which formed one short side of the aquarium. This pane faced a window, and when spring advanced, the growing daylight drew the leaves of the plants in the direction of the pane. So the space forming the territory of the male A gradually decreased in size, and when it had been reduced to an opening between the pane and the plants, only about 3 cm broad, A suddenly abandoned his old territory and invaded that of C, and after some fights succeeded in occupying and holding half of it (Fig. 1 b). Thus, the large territory originally belonging to C was divided into two smaller territories divided from each other by a stone, but both these new territories were larger than the small territory in the glade between the groups of plants still held by the biggest male, B.

3. The Spawning Territories of *Abramis brama*

On June 6, 1950, I had an opportunity of watching the spawning of bream at a point on the shore of Lake Mälaren close to the landing-stage of the Institute. The bottom, which is soft, is at this place covered with a thick carpet of *Myriophyllum*, *Elodea*, and *Cladophora*, and through this carpet *Phragmites* reed of varying thickness shoots up. The width of the belt covered with the above vegetation is about 18 m, but the spawning occurred only within a 5 meter broad zone, parallel with and stretching up to the edge of the *Carex*-covered shore. Within this zone the water temperature along the inner edge was $+23^{\circ}$, in the middle $+19.5^{\circ}$, and along the outer edge $+18^{\circ}$ Centigrade, and the depth 10 cm along the inner and 40 cm along the outer edge. Along the outer edge of the reed the surface temperature of the water was only $+14.3^{\circ}$ Centigrade, which was probably too low for the bream to spawn. That no spawning occurred outside the 5 metres broad zone described above, in spite of the vegetation being of the same type, was thus probably due to the fact that the stimulus summation necessary for the release of the spawning, represented by a sufficiently high temperature and the existence of suitable vegetation, could be reached only within this zone (cf. FABRICIUS 1950).

During this spawning of bream I could fully confirm SVÄRDSON'S observation (1949) that the bream males are strongly territorial in spawning. From the landing-stage we could clearly see six bream males, each of them restlessly patrolling his own limited territory, and farther away we discerned several more territory-guarding males, even though they were more difficult

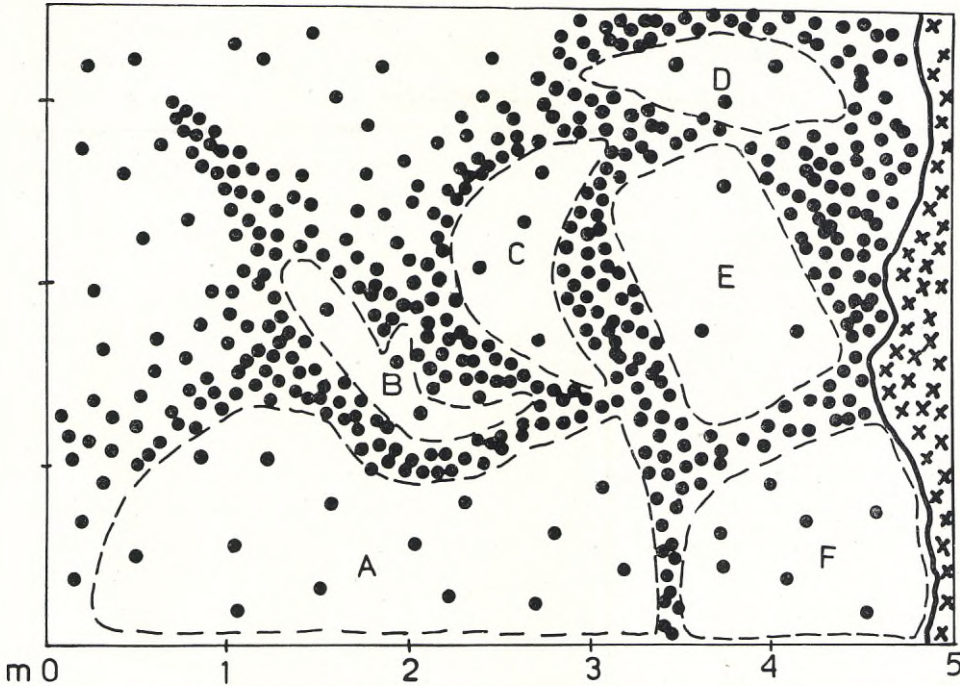


Fig. 2. The territories of six bream males (A—F) in the reeds at the landing stage of the Institute on June 6, 1950. ●●● *Phragmites*, ××× *Carex*.

to see owing to the reflection of the light on the water. Now and then one of the males trespassed on a neighbouring territory and was immediately and violently attacked by its owner, the fight causing a violent splashing in the shallow water. Like SVÄRDSON (op.cit.) I could not observe any lateral display or any other signal movements in connection with the fights between the territory-guarding bream males, but it should be pointed out that the water was not particularly clear and that floating piles of dead lastyear's reed rendered our observations rather difficult. It may be regarded as probable that, in the case of bream, the strikingly restless movement of the males patrolling their territories acts as a threat display against other males, and at the same time as a means of attracting the females to the territory (cf. SVÄRDSON op.cit.). Now and then a female swam through the territory, and then the males — with violent splashing — drove her into thick vegetation, where the actual mating probably took place. But the most violent splashing was — beyond all comparison — caused by the very frequent boundary disputes between the territory-guarding males. It is probably this very splashing that many observers have described as typical of bream spawning (cf., for instance, CURRY-LINDAHL 1945), and it is easy to understand that it may be very intense if hundreds of bream territories lie close to each other within an area with a very slight depth of water.

The six males could be recognized by colour, abundance of pearl organs,

size, and by injured fins. During the period from 9 a.m. to 3 p.m., i.e. as long as the observations lasted, each of these males held the same territory, but it was remarkable how different the territories were in size (Fig. 2). It was particularly characteristic that territories situated in clearly defined glades in thick reed were much smaller than territories situated in sparse, evenly distributed reed. It is worthy of special notice that B, the biggest male furnished with the best developed pearl organs, had a very small territory. Only one of the territories, A, which was situated in sparse reed, was of the size of the bream territories described by SVÄRDSON (op.cit.), about five square metres, the others being considerably smaller.

4. Discussion

WUNDER (1930) established the fact that, in a limited space, only one male of *Gasterosteus aculeatus* will reproduce and that he suppresses all the others; but if the aquarium is divided into several sections by isolating screens, so that the various stickleback males do not see each other, several males can be made to propagate in the same aquarium. This observation was confirmed by TER PELKWIJK & TINBERGEN (1937), who drew the conclusion that the permanent sight of another sexually active male makes an area unusable as a territory for a stickleback male. Similar observations with regard to birds have been made by POULSEN (1950), who has described how two males of the common sandpiper (*Actitis hypoleucos*) each held a territory on either side of a partition — provided with a door — in a pen, but if the two birds were brought together in another pen, where there was no partition, only one of them could hold a territory.

TER PELKWIJK & TINBERGEN (op.cit.) showed, too, that in an aquarium it was possible to displace the boundaries of a stickleback male's territory by moving the groups of water plants that marked those boundaries. Similar observations have been made with regard to several species of aquarium fish (cf. FABRICIUS 1946 a, b).

It is probable that the differences described above between the size of the individual territories of *Tanichthys albonubes* and *Abramis brama* might have some relation to local variations in the grade of visual isolation created by the water vegetation. Territories that are screened off by thick groups of plants, preventing the territory-guarding fish from seeing his neighbours permanently, may therefore be considerably smaller than territories in sparse vegetation where the fish see each other the whole time. It can hardly be a coincidence that the bream territories — observed by SVÄRDSON (op.cit.) — along the comparatively open shore at Sotholmen were as a rule considerably larger than the territories in the thicker reed at the landing-stage of the Institute. In species of animals where — as is evidently the case with most territory-guarding fish and some species of birds — the threat display is chiefly of a visual nature, a considerably larger number of territories may

exist within an area which can be divided by dense vegetation or other ground obstacles into a number of fields, visually isolated from each other, than within an area that is more open and covered with a thinner vegetation. HOCHBAUM (1944) has shown very clearly that this is true in the case of ducks, and PALMER (1941) proved that in the case of *Sterna hirundo* more territories could find room in thick grass vegetation than in thin.

Since — as has been mentioned above — the size of the territory indirectly determines the amount of roe that may be laid on a bottom surface of a given area, a study of these questions may be of some practical importance; particularly when we bear in mind cases where water regulations or other infringements have greatly reduced the spawning areas of economically important, territory-guarding species of fish. In such cases an increase in production might be achieved by establishing a maximum number of territories on the remaining spawning bottoms. From this it would appear that it is of no little practical importance to discover which of our species of fish are territorial, and that it would be desirable to study the spawning behaviour also of other fish.

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Movements and Age of Trout *Salmo trutta*, LINNÉ, in Lake Storsjön, Jämtland

By K. J. GUSTAFSON

Introduction

For the purpose of obtaining more accurate information on the migration of trout in Lake Storsjön, in the province of Jämtland, a preliminary control of the upstream spawning run was operated in the main spawning stream, Dammån, during the summer of 1950. Dammån enters Lake Ockesjön in the south-east, just above its outlet in the north-western part of Lake Storsjön. The distance from its mouth to the upper spawning grounds, in the Oviken Mountains, is about 40 kilometres and the height difference some 100 metres. The water is usually extremely clear and had a pH-value in July of about 7.

At a fish-ladder at Åhn, 12 kilometres above the mouth of the river, the main characteristics and duration of the spawning migration were observed: all trout moving upstream were examined as to length, weight, sex and age, tagged and released above the ladder. During the downstream movement no observations were made as the ladder was not used by the fish at that time.

Migration

The control at the fish-ladder at Åhn was operated during the four months from June 15th to October 15th 1950 (Fig. 1.). The first trout moving upstream was captured on June 24th and the last on September 25th. During this period of exactly three months a total of 872 trout, 263 males and 603 females were examined. Sex was not recorded in six cases. As shown in Table 1, the main run occurred in July and August. The peak was reached between August 6th and 12th (Table 2), during which period the maximum daily catch of 43 trout was also made (Fig. 1.).

The intensive commercial fishing with iron fyke-nets in Dammån below the fish-ladder had a marked effect on the frequency of trout entering the ladder on the different days of the week. This fishing is permitted from 6 p.m. on Mondays to 6 p.m. on Fridays until September 1st, when all

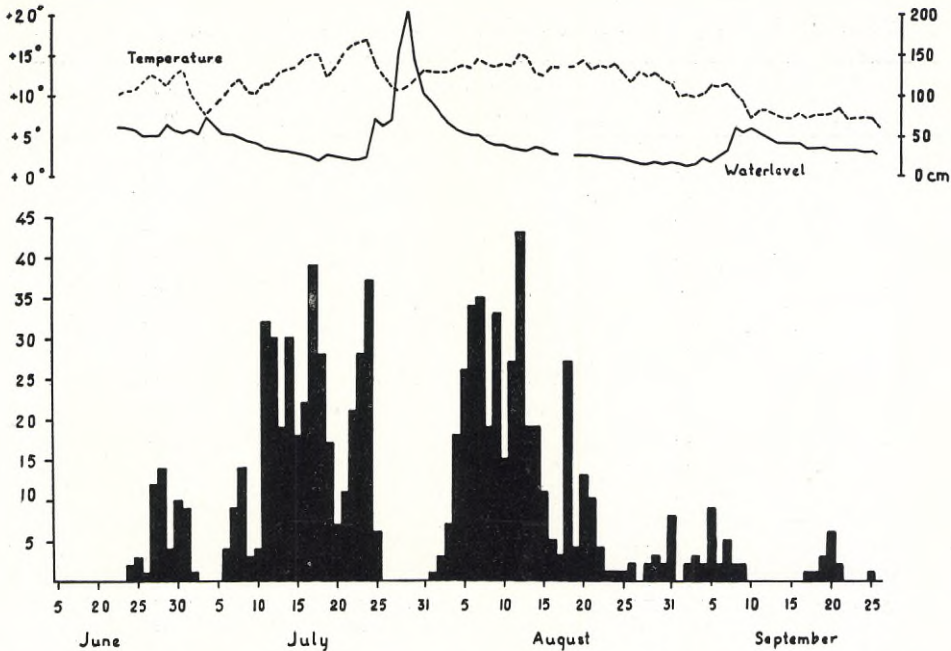


Fig. 1. Water temperature 8 a.m., water level 8 a.m. and daily catches in the fish ladder at Åhn during upstream run 1950.

fishing is prohibited in the stream. The average number of trout caught on each day of the week during the migration up to September 1st, is shown in Fig. 2. A minimum average catch of 6.8 trout was registered on Tuesday and, as might be expected after two days without fishing, the maximum average catch of 14.7 trout was made in the ladder on Monday. When the influence of fishing is so marked, it is difficult to study the dependence of the spawning run on different weather conditions. However, the swift rise in the water level in late July, caused by heavy rains evidently delayed the

Table 1. Monthly catch of trout in the fish ladder at Åhn 1950.

Month	Total number of trout caught	Number of males	Number of females
June	46	14	32
July	389	130	259
August	396 ¹	108	282
September	41	11	30
Total	872	263	603

¹ Sex not recorded for 6 specimens.

Table 2. Weekly catch of upstream trout in the fish ladder at Åhn.

Date	Total number of trout captured	Number of males	Number of females
June 18—24	2	—	2
June—July 25—1	53	16	37
July 2—8	28	8	20
9—15	136	40	96
16—22	145	55	90
23—24	71	25	46
July—Aug. 30—5	55	13	42
Aug. 6—12	206	57	149
13—19	88 ¹	20	62
20—26	32	10	22
Aug.—Sept. 27—2	17	8	9
3—9	25	9	16
10—16	—	—	—
17—23	13	2	11
24—30	1	—	1
Total	872 ²	263	603

¹ Sex not recorded for six fish.

² 6 sp. sex not recorded.

fish moving upstream. No fish entered the ladder from July 26th to 31st (Fig. 1.); the part of the high-water period when the water was extremely muddy. This observation is of some interest when judging the influence on fish of muddiness caused by excavation for water regulating purposes. — The upstream run started at a water temperature at 8 a.m. of $+10^{\circ}$ C, reached a peak on August 12th at $+15^{\circ}$ C and ceased at $+6^{\circ}$ C, the minimum temperature during this season. The maximum of $+16.8^{\circ}$ C was reached on July 24th (Fig. 1.). — The sex ratio in a total of 866 trout was 229 females per 100 males. However, this ratio varied during the course of the migration as follows:

June	July	August	September
229 : 100	200 : 100	260 : 100	270 : 100

It is clear that the predominance of females was greater during the later part of the spawning run.

Among the fish examined in the ladder a remarkably large number, about 16 per cent, showed signs of previous attempts at capture either with the iron fyke-nets in the lower Damman or with hooks. The iron fyke-nets are not satisfactory: every eighth trout passing the ladder showed injuries caused by this gear. The dorsal fin was often removed entirely or in part,

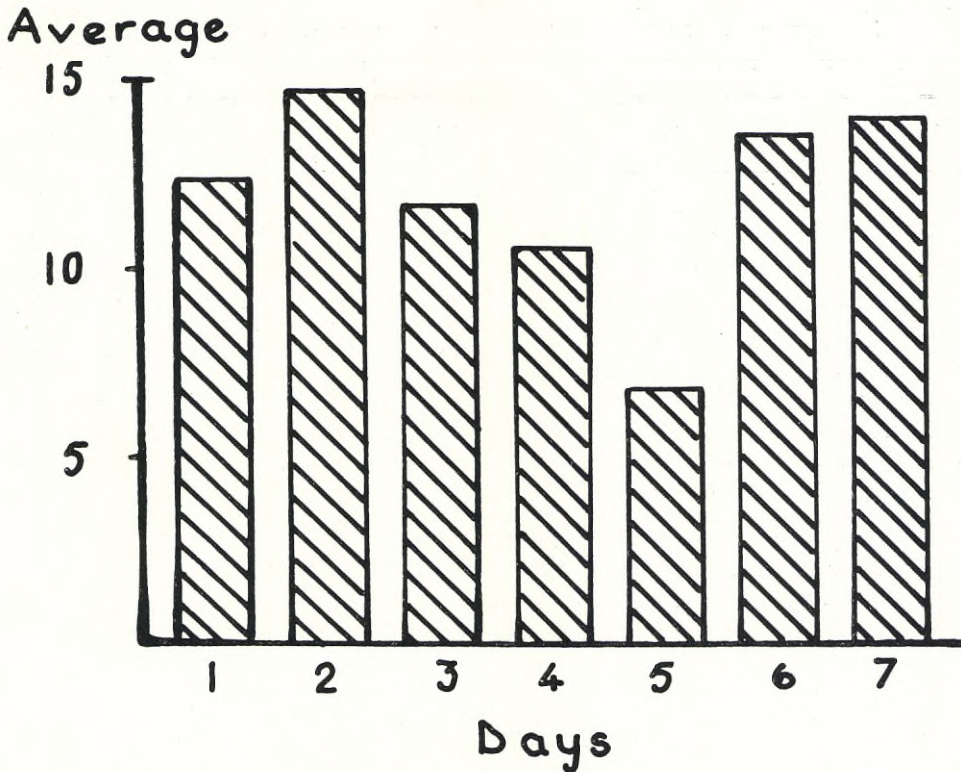


Fig. 2. Average number of trout captured in the fish ladder at Åhn on each day of the week during the period June 23—August 31, 1950.

and a large number had wounds in the sides, these wounds being easily attacked by fungi.

For the purpose of obtaining information on the migration speed and the loss of the spawning stock caused by fishing in the lower Dammån, a temporary trap was built on July 23rd at the mouth of the river at Ytterocke. After two days, unfortunately, the trap was destroyed by the swiftly rising water. During this period six trout were tagged and later, between August 19th and 27th, when another attempt was made, a further six trout were tagged. Of the twelve trout tagged, four were controlled in the ladder. Migration speeds on the upstream run from trap to ladder, were as follows:

Tag No.	Date tagged at trap	Date controlled at ladder	No. of days	Km/day
Sb 3632	July 24	Aug. 18	26	0.460
» 3634	» 25	» 29	36	0.333
» 1540	Aug. 20	» 28	9	1.333
» 1542	» 21	» 30	10	1.200

Table 3. Number of trout entering the fish ladder at various periods of the day during upstream run between June 24 and September 25, 1950.

Periods	Number of fish	% fish per period hour
20 ⁰⁰ —08 ⁰⁰	340	17.5
08 ⁰⁰ —12 ⁰⁰	95	14.7
12 ⁰⁰ —16 ⁰⁰	270	41.9
16 ⁰⁰ —20 ⁰⁰	167	25.9

As shown above, the time between tagging and control was about three times as long for the trout tagged in July as for those tagged in August. Probably these were delayed by the muddiness of the swiftly rising water in late July.

The fish ladder was emptied every 4th hour from 8 a.m. to 8 p.m. Table 3 shows the rate of the upstream migration at the different periods of the day. The maximum, 41.9 per cent, was observed between 12 noon and 4 p.m. and the minimum, 14.7 per cent, during the period 8 a.m. to midday.

Tagging

Tagging experiments were carried out in the Dammån as early as 1938 and 1939, when ANDERSEN and OLSÉN tagged 12 trout: one of these fish, tagged on November 5th 1939, was reported in the southern part of the lake Storsjön on June 7th, 1940, some 60 kilometres from the tagging place. Silver tags attached to the dorsal fin were used.

In 1947 LAPPEA tagged 42 trout from the same river with celluloid discs attached at the base of the dorsal fin. Seven recaptures have been recorded, the first in the lower part of the Dammån only two days after tagging. Three trout were caught in May 1948 at Ytterhallen, Hallen and Trappnäs, all about 30 kilometres from the tagging place. Two specimens were reported at Trångsviken, one in June and one in August 1948. It is of interest that the last trout recovered, male, was caught on August 28th 1948 in the river Storboströmmen, another spawning stream of the trout from lake Storsjön.

Finally, 25 trout were tagged by SJÖBLOM in 1949. One of these fish was caught on August 7th 1950, in the northern part of the bay Brunflöviken, about 60 kilometres from the place where tagged.

From June 23rd to October 9th, 1950, a total of 874 trout were tagged in the Dammån, 861 specimens at Åhn and 13 specimens at Ytterocke. All except one were tagged on the upstream run. The fish were tagged in 759 cases by attaching a celluloid disc at the base of the dorsal fin, and in 114 cases

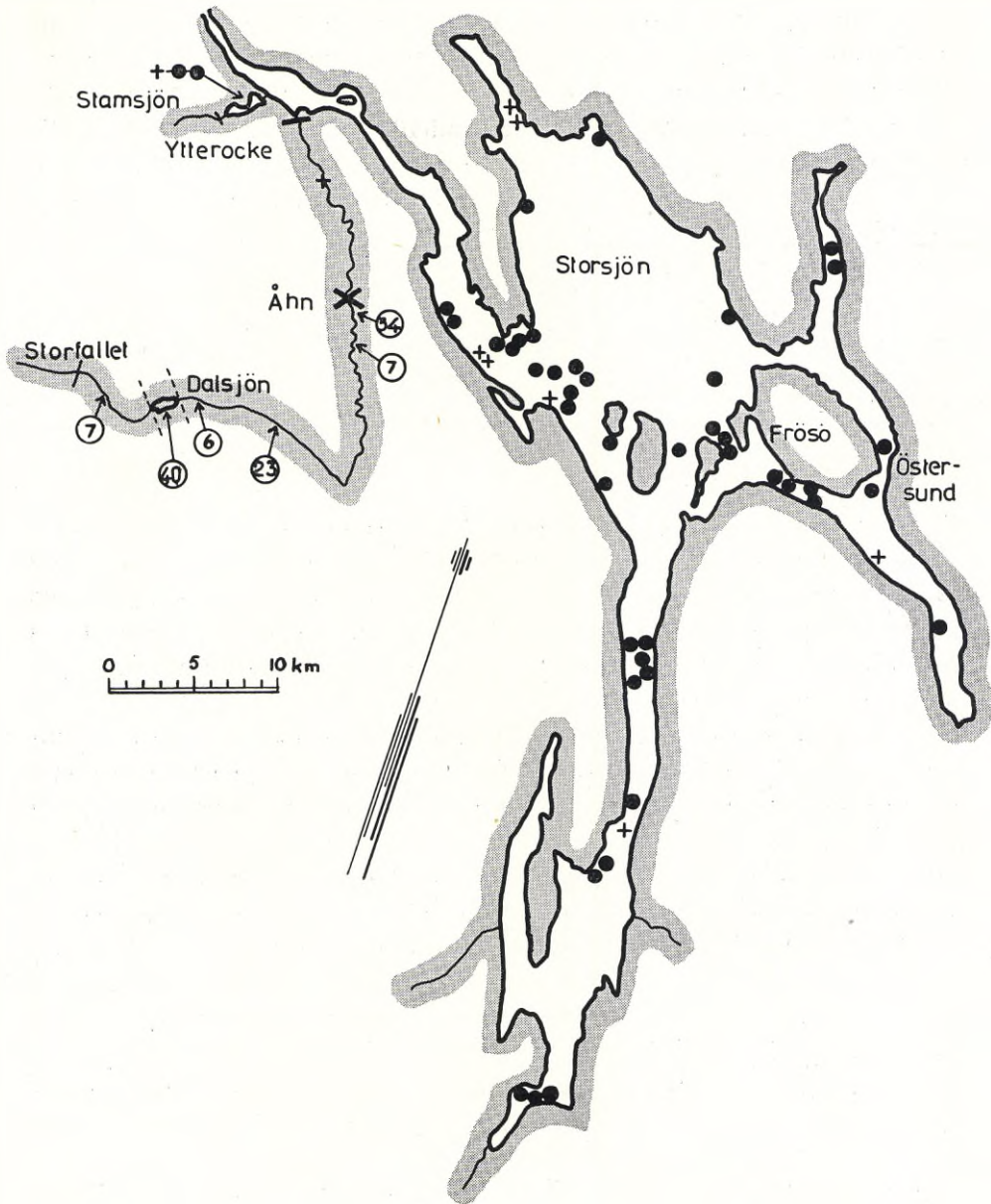


Fig. 3. Trout tagged in the fish ladder at Åhn (×) and in the trap at Ytterocke (—) during the summer of 1950, recaptured in Dammån (O with number of fish recaptured), Lake Stamsjön and Lake Storsjön (●=one fish recaptured). Recoveries from earlier taggings at Åhn marked with +.

by clipping a silver tag onto the upper part of the tail fin. Both methods included the removal of the adipose fin in order to ensure recognition of the 1950-spawners at the control in the ladder during the following years. — Up to June 10th 1951, 161 trout, 57 males and 104 females, were reported; the majority, 117, in the Dammån, 2 in Lake Stamsjön and 42 in Lake Storsjön (Fig. 3.). The numbers of trout recaptured each month from June 1950 to June 1951 are as follows:

	1950								1951					
	Total	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Febr.	March	April	May	June
River Dammån	117	2	23	70	16	5	—	—	—	—	—	—	1	—
Lake Stamsjön	2	—	—	1	—	1	—	—	—	—	—	—	—	—
» Storsjön	162	—	—	—	—	6	15	1	1	4	—	—	7	8
	161	2	23	71	16	12	15	1	1	4	—	—	8	8

Of the 117 trout tagged and recaptured in the Dammån 34, or about 30 %/, were caught in two iron fyke-nets 500—800 metres above the ladder the same day as tagged or a few days later. However, one trout remained 43 days in the river before being caught in the fyke-net 500 metres upstream the tagging place. The remaining 36 trout, recaptured between the fish ladder and Lake Dalsjön, were caught by fishermen, chiefly in August.

40 tagged trout were reported in Lake Dalsjön, caught both in nets and by fishermen. This lake is the only point in the Dammån at which fishing is permitted after September 1st, and the last recapture was made here as late as October 27th.

In the upper part of the Dammån, from Lake Dalsjön to the falls, Storfallet, the natural obstacle in the upstream run, seven trout were recaptured, all by fishermen. The recoveries from the different parts of the Dammån in 1950 were as follows:

	Ladder-Lake Dalsjön Fyke nets	Lake Dalsjön Sportfishing	Lake Dalsjön	Lake Dalsjön— Storfallet
June	2	—	—	—
July	18	2	2	1
August	14	34	16	6
September . .	—	—	16	—
October . . .	—	—	5	—
Total	34	36	39	7

Two recaptures of interest were reported from Lake Stamsjön in the Storböströmmen which, after the Dammån, is the most important spawning stream for the trout from Lake Storsjön. These two, both males, were tagged at Åhn on the upstream run on July 14th and August 13th, and recaptured

on August 30th and October 23rd, respectively. The male captured in October had flowing milt. As this fish was tagged as late as August 13th, the extraordinary flood mentioned above, cannot have influenced the change in the spawning stream, as might be true in the case of the first one tagged in July.

Including the recovery of the 1947 tagging, a total of three male trout tagged in the Dammån were recaptured in the Storboströmmen, either in the tagging year (2) or the following year (1). More accurate information about this wandering between different spawning streams will, I hope, be recorded during 1951, when a trap is to be built at the mouth of the river Storboströmmen.

From Lake Storsjön 42 tagged trout were reported, the first on October 22nd and the last one on June 10th, from all parts of the lake. The recoveries in the southern end of the lake were about 86 kilometres away from the tagging place. The tagging experiments show that at least 116 trout, or 14 per cent of the 831 specimens passing the ladder, were caught in the Dammån upstream the ladder during this spawning season.

Fourteen (12.2 %) of the 114 trout tagged with silver were recaptured, and 145 (19.6 %) of the 759 trout tagged with discs. Evidently the silver tags were not so satisfactory for trout as the discs, most probably due to their marked tendency to cut out along the fin rays and loosen even a few days after being affixed.

On the downstream run two trout were recaptured at exactly the place where they had been tagged on the upstream run. One fish caught on October 8th, and one the following day, were tagged on August 13th and July 21st, respectively. They thus stayed 57 and 81 days on the spawning ground.

Age

An analysis of scales from 644 trout showed a distribution in the different year classes as follows:

	Year 5	6	7	8	9	10	11	12	13	14
Number of trout	1	17	101	238	160	88	32	5	1	1

Obviously about 90 cent of the spawning stock were seven to ten years old.

As regards the time the trout spend as young in the river before their migration down to the lake, an analysis of 614 scales was made with the following result:

	Year 2	3	4	5	6
Per cent of the total	4	19	47	27	3

Thus the majority of the young trout spend four years and 46 per cent three or five years in the river where hatched.

Summary

A study of the trout migration in a spawning stream, Dammån in Jämtland, was made during the summer of 1950. The information recorded was as follows:

1. A total of 872 trout moved upstream from June 24 to September 25.
2. The migration mainly occurred in July and August. A peak was reached between August 6 and 12 with a maximum daily catch of 43 trout.
3. About 40 per cent of the total trout captured were caught between 12 noon and 4 p.m.
4. The maximum migration speed was 1.3 kilometres per day in the lower part of the stream.
5. Swiftly rising water in the stream had a pronounced negative effect on the intensity of the migration.
6. The sex ratio of 866 trout was 229 females per 100 males.
7. Tagging experiments show that trout spawning in the Dammån are coming from all parts of Lake Storsjön.
8. Tagging with celluloid discs at the dorsal fin shows 19.6 per cent recovered and that with silver tags at the tail fin 12.2 per cent recovered up to June 1951.
9. Three trout, tagged at the Dammån, have been recaptured in another stream during the same spawning season as tagged (2) or during the following (1).
10. About 90 per cent of the spawning stock were seven to ten years old and about 50 per cent spend as young four years in the stream.

Nylon contra Cotton

By GÖSTA MOLIN

The author of the present paper has previously (MOLIN 1950) given an account of the results of the investigations carried out since 1947 at the Institute of Freshwater Research with a view to establishing the fitness of nylon thread for the manufacture of fishing-tackle for various purposes. These investigations included similar experiments with cotton yarn in order to determine the differences in strength and serviceableness under various conditions.

One of the most valuable qualities of nylon thread is its absolute constancy against rot, its eminent suitability for snaring tackle, and its great strength. These properties are very different from those of cotton yarn. A less attractive quality, however, was the consistency of the thread used which made it very difficult to get the knots of the ready-made tackle to hold, and consequently it lent itself but unwillingly to really serviceable fishing-tackle. The knots tended to slip even in tackle which was not in use. It should, however, be pointed out that the thread available for the experiments — with the exception of the solid-drawn nylon thread — was not intended for fishing-tackle in particular, but had been picked out at random among the various types of thread available for textile purposes. We also noted the quality typical of all nylon thread, *viz.* that after some time in water — 10 to 24 hours — it decreases in strength by 15—30 %. After that time no further decrease in strength occurs: the strength of the thread remains constant. Tests with knotted threads made it clear that nylon thread is considerably more sensitive to knotting than is cotton yarn, and for nylon the decrease in strength was 24—43 %, whereas the figures for cotton did not exceed 10—35 %. Tests with nylon gill nets resulted in catches three times as big as those of cotton gill nets of the same size and meshes.

During 1950 the situation on the »nylon front» has become considerably brighter, and it has been possible to import spun nylon thread especially intended for fishing-tackle. Further experimental manufacture of fishing-tackle of solid-drawn thread has not been considered urgent as the consistence of that thread does not yet allow of a mechanical manufacture of nets.

The spun thread that has been tested during the recent phase of the

experiments has been of French, American, and German origin. As was the case in the earlier experiments, the different types of thread have been tested under various conditions with a view to establishing their strength in dry, wet, and knotted condition and, furthermore, test fishing has been carried out in several lakes with the ready-made tackle. Below is a description of the properties of the different types of thread, and details on their suitability for various kinds of fishing-tackle.

French nylon. In the autumn of 1950 a consignment of spun nylon thread marked $75 \frac{2}{3}$ was imported from one of the big textile firms of France — T. SCHMIDT of Paris — and a number of unmounted nets with different mesh sizes were made of this nylon at »Laxens Fiskredskapsfabrik» at Umeå. The knots — especially in the fine-meshed nets — tended to slip, however, without any external influence. This fault was corrected by having the nets restretched with the aid of pulleys, whereupon they were immediately fixed in boiling water. This treatment proved most successful, and no slip-meshes could be found during the following test. The necessity for this after-treatment can probably be explained by the fact that the French nylon then available was comparatively stiff, which prevented the knots being drawn tight enough. This was later brought to the attention of the French firm, and judged by samples which have recently been received, nylon thread of more recent manufacture is very soft and supple.

The test fishing was carried out in Lake Mälaren with nylon gill nets of a mesh-size of 11 stretched meshes/ell, and in Siljan in Dalecarlia and Brunträsket in Västerbotten with $6 \frac{1}{2}$ — $7 \frac{1}{2}$ stretched meshes/ell. In Lake Mälaren the fish caught were perch and roach, and in the two other lakes *storsik* (a big form of whitefish) and burbot. In all three places parallel tests were made with cotton gill nets of the same size and mesh-size in order to obtain comparable figures of the efficacy of the different types of nets. The result of the tests was that 18 nettings in Lake Mälaren gave twice as much fish in the nylon nets, 17 nettings in Siljan almost three times as much, and the same number of nettings in Brunträsket somewhat more than twice as much in the nylon as in the cotton nets. Thus the nylon nets proved their worth in a convincing way and the figures would probably have been even better if the yarn in the fine-meshed nylon nets had been still finer. For the consignment of yarn imported consisted of only one size, which was suitable for the coarse-meshed nets but which was too coarse for the fine-meshed ones. — Fyke-nets were also made — on a smaller scale — by hand, of coarser French nylon thread. They have not yet been tested in practice but the knots seem to hold well without any particular fixing. It is now possible to import the French thread in all dimensions, from very fine up to coarse; this coarse thread can also be used for the top and bottom lines in gill nets.

The stretchability of the French nylon thread is 25—45 % of the length,

whereas the corresponding figures for cotton yarn are 10—23 %. In water the decrease in strength is 5—30 % of dry thread, which is a high figure if we bear in mind that the strength of cotton, on the contrary, *increases* by 11—31 % when immersed in water. The strength of French nylon knotted thread decreases by 30—48 %, whereas the corresponding figure for cotton does not exceed 10—35 %.

American nylon. In 1950 it was possible to import this thread from England as unmounted nets. The thread, *i.e.* the raw material, is manufactured in America, whereas the knotting is done in England. This type of nylon net is without doubt the best available at present. The thread is very soft and supple, and the knots hold without any special after-treatment. Evidently American factories have a special method of treatment of the raw product in order to make the ready-made material immediately fit for fishing purposes, but this method is being kept a total secret and it has not been possible to obtain any information regarding the procedure. So when using other types of nylon we must, if necessary, make use of the above-mentioned fixation, which proved to be quite effective in the case of the French nylon. During 1950 quite a few fishermen tested the American nylon nets which, without exception, have been praised for their great efficacy. The result of the tests made by the Institute was that 10 nettings with the American nets mounted as gill nets gave three times as much fish as the cotton gill nets laid out at the same time.

The two sizes of thread that have been available so far were marked N6 and N12 and correspond to the cotton yarn sizes 80/6 and 60/9, respectively. The strength of the American nylon is considerably greater than that of cotton yarn, but instead it is remarkably sensitive to knotting, and the decrease in strength of wet knotted thread is no less than up to 60 % of that of dry thread without knots. Moreover, the American nylon thread has another property which distinguishes it from other makes: its poor elasticity, which is no more than 17—18 % of the length of thread, a figure not much higher than the corresponding figure for cotton yarn. It may be that the poor elasticity is one of the reasons why the knots are so stable. The American factories are now producing threads in sizes which may be suitable for coarser fishing tackle, but only small samples of such sizes have reached us so far, and it has therefore been impossible to test them.

German nylon (perlon). The consistency of the German nylon thread is quite different from that of other types of nylon thread. The above-mentioned types are without exception made of long fibres, *i.e.* the thread is spun of extremely fine and interminably long fibres, which makes the finished thread absolutely even in thickness, with a very smooth surface and comparatively even and tough in strength. The German *perlon* yarn, however, is manufactured in the same way as cotton yarn. Thus, the nylon fibre is chopped into short pieces, whereby so-called nylon wool is obtained, of which the

thread is then twined. Consequently, a feature characteristic of the *perlon* yarn is that it does not differ very much from cotton yarn in appearance and, like cotton yarn, its surface is full of short protruding ends, which gives it a woolly appearance. Its strength is lower than that of nylon thread made of long fibres but considerably greater than that of cotton yarn. It should also be pointed out that the strength of *perlon* is rather uneven, that of nylon thread made of long fibres is very even. The stretchability of *perlon* thread is comparatively great: about 52 % of the length of thread. When the thread is immersed in water, the decrease in strength is between 5 and 20 %. As regards sensitiveness to knotting it can be compared to French nylon thread; the decrease in strength is 22—41 % of that of thread without knots.

On account of its consistency German *perlon* is very suitable for binding fishing-tackle, and the knots hold without any special fixation. A contributing factor is no doubt its rough surface. The woolly surface has one disadvantage, however, and that is that particles of mud easily stick to the thread and are more difficult to wash away than in the case of the nylon thread made of long fibres, on which mud and other impurities do not stick so easily.

The practical tests with fishing-tackle of *perlon* consisted of fishing with fyke-nets for pike during the spring of 1950. The experiment proved satisfactory in so far as the knots did not slip under the strain to which they were subjected. On the other hand, the thread was not sufficiently strong for big pike; when the tests were started no *perlon* coarser than 40/9 was available. Now there are several threads of larger sizes, the strength of which is quite satisfactory for our purposes. During 1950 such tackle was in use at several places in this country. According to reports from fishermen the thread proved fairly good for the binding of the nets and the knots evinced no tendency to slip, but from some quarters complaints have been made that the thread of the inner part of fyke-nets intended for catching pike-perch, was fairly easily cut through by the sharp gill-covers of the fish. This may be explained in part by the small dimension of the thread, but it may also be that the resistance of *perlon* against such damage is not great. Continued practical tests during the next season will doubtless throw light upon this matter. The nylon thread made of long fibres, on the other hand has, according to the Germans, great power of resistance against mechanical wear. The Germans have not manufactured long-fibred *perlon* of the American and French types until the last few months, and only samples of such thread have been available. It will probably only be a matter of time before this thread is produced on a large scale.

In all the tests the catches have been considerably bigger with nylon gill nets than with corresponding nets of cotton. The chief reason is no doubt that nylon gill nets »behave» better in water than cotton nets. For nylon has a low specific weight, and moreover it does not absorb water to the same extent as cotton, which absorbs a great deal of water. Furthermore, nylon

retains its original thickness in water, whereas cotton swells somewhat, which influences its snaring capacity, the latter being to a large extent dependent on the size of the thread. The thinner the thread, the greater is the efficacy of the nets. It may also be that the great elasticity of nylon thread is a factor that contributes to its high catching propensity, but, on the other hand, we have the American nylon nets with comparatively low stretchability.

The nylon used in these tests has, without exception, been white, uncoloured, and as such thread is generally supposed to be less efficient, we have tried to dye French nylon and German *perlon* with various dye-stuffs. It proved difficult to make the tannins »katechu» and »Weibull catch» take on the French thread, whereas *perlon* turned light-brown. Anilines, on the other hand, took very well on *perlon* and French nylon, and the thread obtained the shade of colour required. Of these anilines, only »Eken» fishing-tackle dye has been used so far on French nylon, and after 20 nettings the shade has not changed noticeably. Nor do burbot nets of *perlon*, on which this dye has been used, show any change of colour after having been immersed in water for a month and a half. It may also be mentioned that all types of dyestuff seem to take more easily on *perlon* than on nylon thread made of long fibres. There is now on the market a dyestuff specially for dyeing nylon fishing-tackle, but the price is no less than 80 Swedish kronor a kilo, and it has not been tried in practice.

As has been stated above, nylon thread — with the exception of the American — has very great elasticity and this influences the mesh-size in the manufacture, when the meshes shrink by about 10 %. If, for instance, the net machine is adjusted for a mesh-size of 10 stretched meshes/ell, the finished net will be 11 stretched meshes/ell, etc., and moreover the length and depth of the net will be reduced by 10 %. But as this fact is now known, it will be a simple task to obtain the mesh-size required by adjusting the machine.

In discussions about the prices of nylon tackle as compared with corresponding cotton tackle, it has often been pointed out that nylon is so expensive that it will not pay to change over. I do not think, however, that we need be so hesitating on that point, especially with regard to fine thread intended for various kinds of nets. Cotton yarn 120/6 is at present about 53 Swedish kronor a kilo. If we compare this with French nylon of corresponding strength in wet condition, the price is only 65 Swedish kronor a kilo, so the difference in price is comparatively insignificant. As regards coarser yarn, however, the difference in price is greater. Cotton yarn No. 12 is 12—13 Sw. kronor a kilo, whereas corresponding French nylon and German *perlon* of the same strength is 55—60 Sw. kronor a kilo. Part of this difference, however, is counterbalanced by the fact that in *perlon* there are twice as many, and in French nylon a little more than twice as many metres per kilo as in a kilo of cotton yarn. A most important detail from the economic point of view is that nylon thread does not rot, whereas fishing-tackle of cotton

has a comparatively short length of life even if one tries to lengthen it by impregnation, which is often an expensive process. It may be claimed that a fisherman whose fishing-ground is so situated that he need not risk destruction of his fishing-tackle by storms or other natural catastrophes would, in the long run, lower his costs by using nylon tackle. If we then take into consideration the fact that catches made with snaring tackle of nylon are twice or three times as big as those of corresponding cotton tackle, a change to nylon tackle would seem to be anything but prohibitive.

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The Population of Char, *Salmo alpinus*, LINNÉ, in a Regulated Lake

By SVEN RUNNSTRÖM

In the last few years a large number of lakes in the north of Sweden have been dammed up in order to give a more even water-supply to the power-generating stations built in the rivers. In those regulated lakes great variations of the water-level occur, which affect the stock of fish and the production of food suitable for fish. The Institute has an extensive program with a view to studying the effect of these regulations on the fishing, and in one of the lakes, Torrön in Jämtland, continuous observations have been carried out since 1938.

Torrön, which is one of the source-lakes of Indalsälven, is situated 410 metres above sea-level. The area of the lake is 95 square kilometres, and its greatest depth is 108 metres. The lake is of the oligotrophic type and has only a sparse bottom vegetation in shallow inlets, consisting chiefly of *Isoetes lacustre*. The amount of fish caught in the lake is very low, only about 0.5 kg per hectare.

The stock of fish consists of char, trout, grayling and burbot. Of these, char is the most important for fishing, especially during its spawning time in the autumn.

The level of Lake Torrön was raised by 7.5 metres in 1937, a dam then being constructed at the outlet of the lake, and in 1940 the level was raised to 8.25 metres. In the winter of 1939—1940 the water-level was lowered to 4.6 metres under normal low water-level. Thus, the total variation in the water-level is 12.85 metres. By the regulation a storing capacity of 1.221 millions cubic metres has been obtained. Fig. 1 shows the variations in the water-level after the regulation during a year with a normal afflux of water.

The char spawn in September. Before the regulation, the spawning took place on stony bottoms along the shores and on reefs in the lake, and also on the *Isoetes*-bottoms at a depth of about 2—8 metres.

After the regulation the spawning occurs when the water-level is highest, whereas, at the time of the hatching of the eggs in the spring, the water-level is lowered to its lower limit (Fig. 1). The fishery expert at the time supposed that a great deal of the char spawn would be laid dry and killed in the

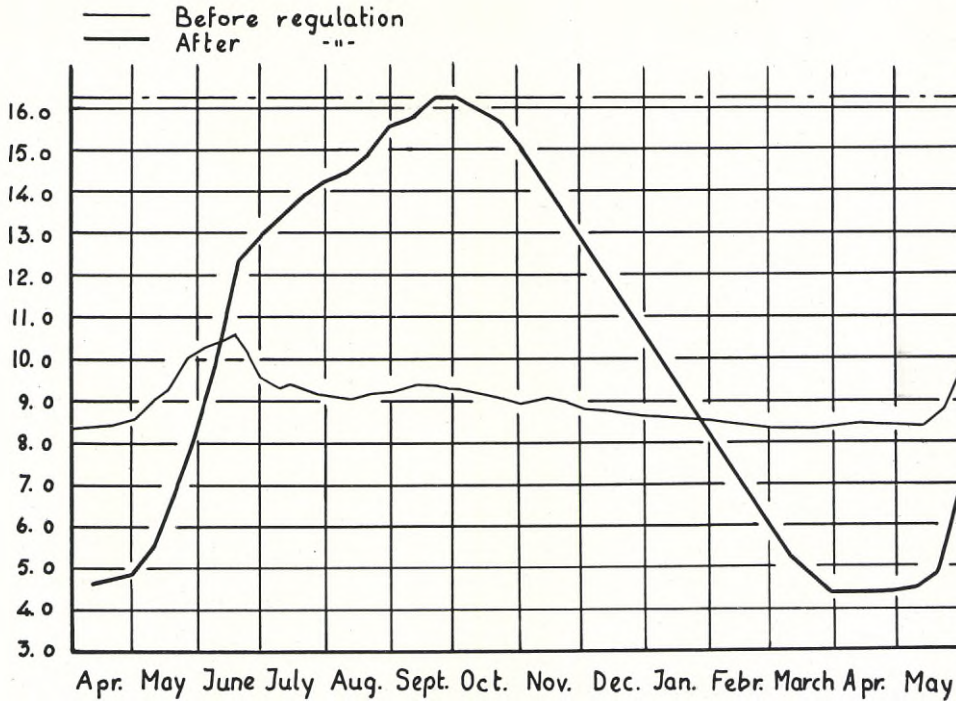


Fig. 1. Water-level variations in Lake Torrön before and after regulation.

winter and that consequently the stock of fish would be so much reduced as to render fishing unprofitable. He supposed, too, that there would be great difficulties in obtaining enough spawn with which the stock of fish might be maintained by fish-culture.

In the following pages I shall give an account of the influence of the regulation on the stock of char during the last fourteen years. Since 1937 records have been kept by some fishermen of the catchings during the spawning of the char, and since 1938 samples of scales have been taken from the spawning fish in order to establish the age and growth of the char. Moreover, samples of stomach contents have been taken and quantitative investigations of the bottom fauna have been made.

As regards the spawning places of the char, the *Isoetes*-vegetation has disappeared altogether owing to the high water-level in summer and the draining in winter, and these bottoms have now lost their importance as spawning places. In spite of the greater depth, the char spawned at the old spawning places during the first few years. On the new dammed-up parts of the shores, however, the earth has been eroded away at the places exposed to the wind, and the stone- and gravel-bottom now laid bare offers suitable spawning places which have also been occupied by the char. FABRICIUS (1950) has later made the same observation at Lake Storsjouten, and it would seem

that the spawning is more dependent on the nature of the bottom than on the depth. At Lake Torrön the spawning of the char thus has a considerably greater vertical distribution after the regulation than before.

Fig. 2 shows the vertical distribution of the spawning char on a spawning ground in September, 1945. A long chain of gill nets was laid from the edge of the ground down to a depth of 16 metres. When the nets were brought up, soundings were taken and the fish caught in each net were counted. The piles show the percental distribution of the catchings at various depths, and we may assume that they also give some idea of the distribution of the spawn laid. Some critical water-levels have also been included in the diagram.

What happens to the spawn in winter when the water-level is lowered? That largely depends on when the hatching occurs. In order to investigate this problem boxes containing newly fertilized spawn were planted at the spawning places and controlled during the winter. The tests showed that the hatching occurred as early as from the middle of December to the beginning of January.

Laboratory test showed, too, that most of the char fry which were a few weeks old, were so good swimmers that they were able to follow the slowly sinking water-level without being laid dry. It may accordingly be supposed that even about February 1 the fry in Lake Torrön are so far developed as to be able to follow the water to its lower level in winter. Fig. 2 shows that at this time the water-level had reached +9 metres, and that about 67 % of the fry might be able to save themselves. An investigation of another spawning place situated at the shore, where the char spawned at a depth of 1—15 metres, showed that a somewhat larger part of the spawn, 44 per cent, were probably killed by the draining.

These investigations would seem to indicate that up to 50 % of the char spawn may be laid dry by the water-level variations caused by the regulation. Some years the mortality may be less and other years greater depending on whether the water-supply is rich or poor.

It is now of interest to see how this interference in the propagation of the char has affected the number of fish and thereby the yields of the fishing.

In order to get comparable figures for the yields of various years I have calculated the average yield per unit of effort. The relative yields during the years 1937—1950 are shown in Fig. 3, the yields of 1937 being taken as standard. The yields of 1937 correspond quite well to the figures given by the fisheries inspector for the nineteen-twenties.

If we first look at the number of fish (Fig. 3, top diagram), the yields of spawning fish show a rising tendency during the first few years. The yields sink during the years 1941—1944 and then reach more normal values but with a rather high peak in 1949. Some corrections have been made for the years 1943—1945, as nets with the appropriate mesh size were not available at the time. I shall revert to that question later on.

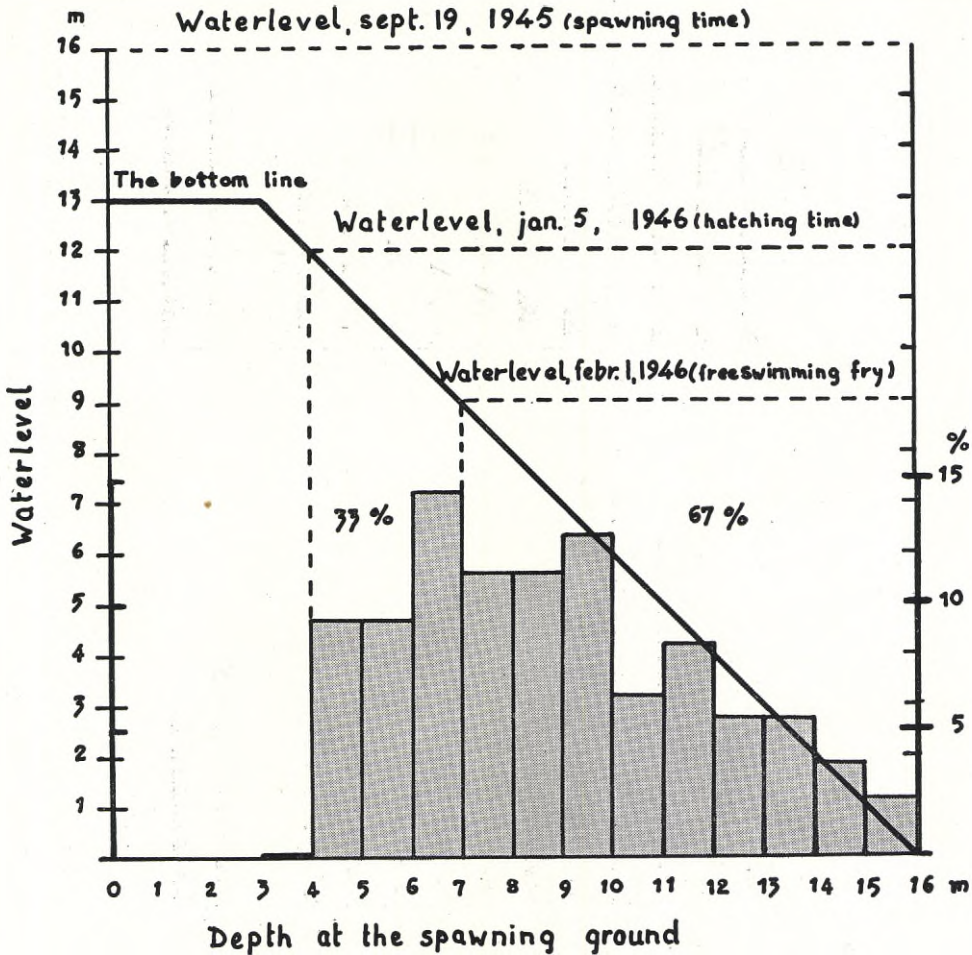


Fig. 2. The vertical distribution of char on a spawning ground on September 19, 1945, and the water-levels at the time of spawning, hatching of the eggs and occurrence of free-swimming fry.

If we take a look at the yields in weight, we are presented with a somewhat different picture. During the first years subsequent to the regulation real record catches were made and the yields of 1940 were almost double the catches before the regulation. Such good yields have not been obtained since, and the yields in weight during the good year 1949 were not by far as good as during the first years.

This phenomenon is due to the changes in the average weight of the char as is illustrated by the bottom diagram in Fig. 3. It appears that the average weight of the char increased during the first years after the regulation owing to the additional food from the shore that the lake was supplied with by

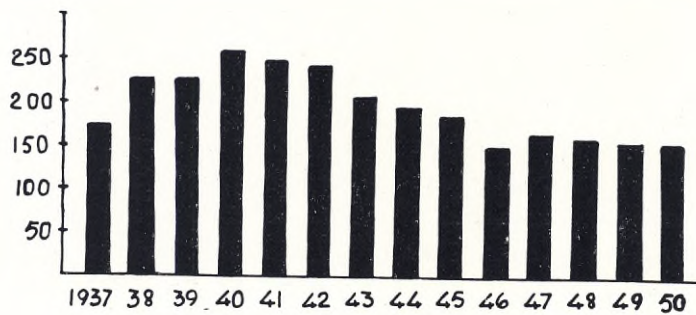
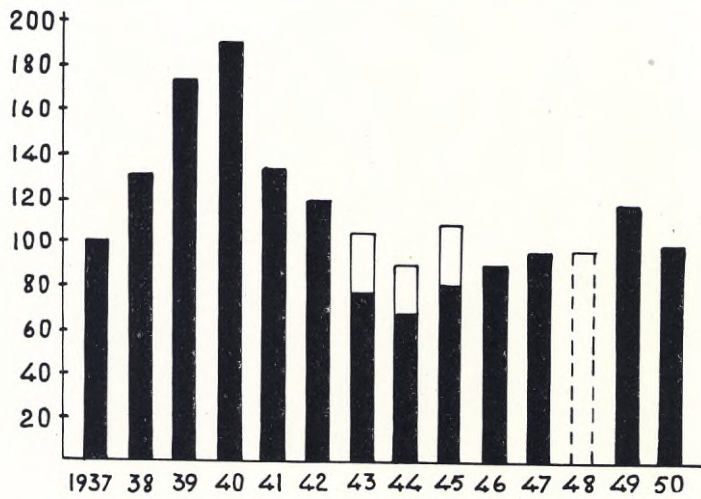
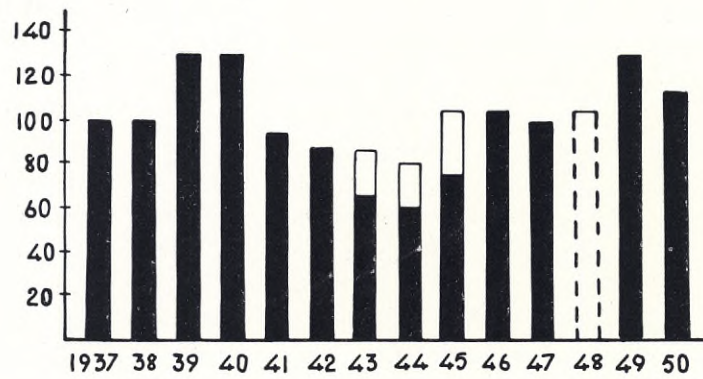


Fig. 3. The relative annual catch of spawning char (the catch 1937=100) in number of fish (above) and weight (medium) during the period 1937—1950, and the mean weight in grammes of the char in the catch (below).

the damming-up. After the shores had been eroded this additional food disappeared, and the average weight decreased more and more and even sank below the original figure.

The diagrams of the yields clearly show that the fishing of the spawning char has not been impaired by the regulation as the expert at that time feared. Occasionally the fishermen have had to find other fishing places but with some variations they have succeeded in getting the same number of fish per net and man as before the regulation.

It is accordingly of great interest to establish whether since the regulation factors have arisen that have been able to neutralize the damage to the propagation. It may be that the regulation was not fully utilized during these years, or that since 1940 the regulation company has planted a considerable number of char fry. To analyse these problems I have used as a basis the age determinations of the spawning char that have been made every year and have calculated the shares of the different year-classes in the yields, as shown by the diagram in Fig. 4. Thus, year-class 1935 originates from the spawn laid in the autumn of 1934 and hatched at the beginning of 1935. Below that diagram I have entered figures showing the lowering of the water-level that the spawn has been subjected to from the spawning in September to February 1.

Year-classes 1935—1937 were not affected by the regulation; 1937 even had a raising of the water-level at the time of the hatching owing to a small damming-up that was made as early as 1936. It is interesting to note that these year-classes, which came into being before the regulation, show quite great fluctuations with two rich and one poor year-class. If we examine the year-classes that were subjected to a lowering of the water-level in winter from the year 1940, we find that the year-classes 1940, 1942 and 1946 were subjected to great lowerings of 7—8 metres with great losses of spawn and fry, whereas, for instance, year-classes 1941 and 1943 were subjected to insignificant lowerings of the water-level, or about 2 metres. There is, however, nothing to show that the former year-classes gave smaller yields than the latter. Year-class 1943, which was subjected to the smallest lowering, even gave the smallest contribution to the fishing.

The bottom diagram in Fig. 4 shows the number of char fry planted. During the period 1940—1944 fry were planted every year. In order to establish the effect of the planting, fry have since then been planted only every second year, and 1945 was the first year that no char fry were planted. If we take a look at year-classes 1940—1944 there may seem to be some correlation between the yields of these year-classes and the number of fry planted. That is, however, completely contradicted by the rich year-class 1945, which received no hatchery support. There is some evidence suggesting that the richness of the 1945 year class was due to high summer temperature (cf. SVÄRDSON 1951). In spite of the fact that in the following year almost

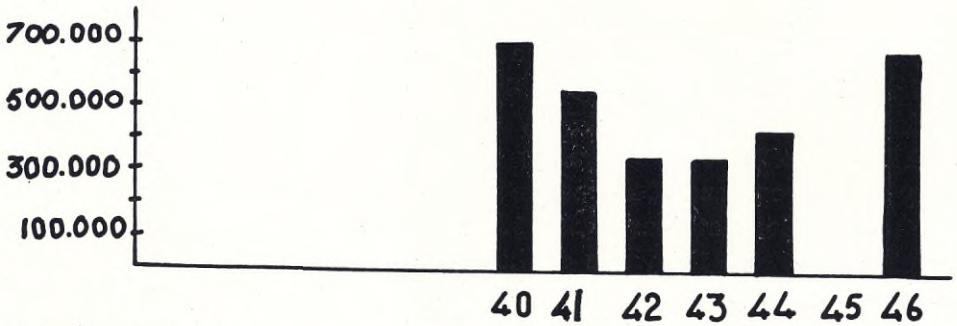
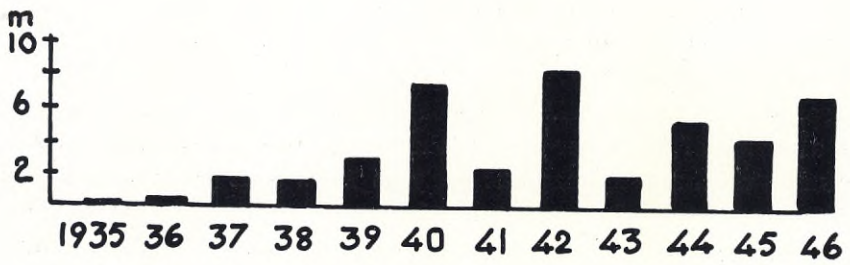
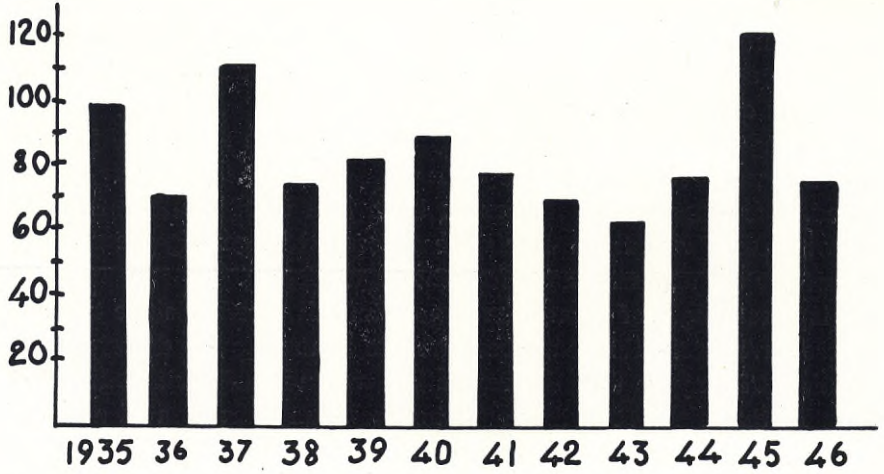


Fig. 4. Relative catches (above) of spawning char of year classes 1935—1946 (catch of year class 1935=100), water-level variations during the incubation of the roe, and number of planted char fry during the period 1940—1946 (below).

Table 1. Length and weight of spawning char, Torrön, during 1938—1950.

Catch year	4 summers old		5 summers old	
	mean length cm	mean weight gr	mean length cm	mean weight gr
1938	28.5	252	31.0	306
1939	28.8	251	32.3	352
1940	29.9	250	34.6	379
1941	30.1	218	34.3	311
1942	29.1	196	32.8	293
1943	27.8	190	31.1	254
1944	—	—	—	—
1945	26.2	—	27.4	—
1946	25.2	160	26.8	188
1947	23.3	148	24.9	173
1948	24.9	140	26.2	166
1949	25.6	137	27.4	184
1950	24.0	—	25.5	—

70.000 fingerlings — corresponding to 700.000 fry — were planted, year-class 1946 was only about 60 % of the size of year-class 1945.

Thus, the conclusion of the above observations is that neither the destruction of spawn by the variations in the water-level nor the planting of fry have had any influence on the variations in size of the year-classes. It is obviously a question of fluctuations due to other causes, which will be found in unregulated lakes too. As long as there is an abundance of spawn and fry, the absolute quantity of spawn is not decisive for the size of the year-class. On the basis of marking experiments it may be estimated that the stock of spawning char in Lake Torrön is of the magnitude of 100,000 fish, half of them being females which produce a total of 25 million spawn. Of this spawn only 0.4 % need develop into catchable fish to maintain the size of the stock. The surplus of spawn is so great that if about 50 % are lost by draining, the result will nevertheless not be affected; on the contrary, the reduced number of fry will experience better conditions owing to decreased competition. Nor can, under these conditions, an addition of hatchery produced fry have any influence on the size of the stock. These results are in harmony with MILLER's (1946) experience with regard to the effectiveness of planting of whitefish fry.

If, accordingly, the regulation has not affected the production of fish in Lake Torrön, a change in the average weight of the char has nevertheless occurred, as appears from what has been said above and is illustrated in Fig. 3, and I shall give further particulars of this phenomenon in the following pages.

Table 1 shows lengths and weights of spawning char four and five summers old from the period 1938—1950, during which time samples of scales were taken. It appears that both the length and weight of the char increase from 1938 and reach a maximum about 1940—1941, after which time a continuous

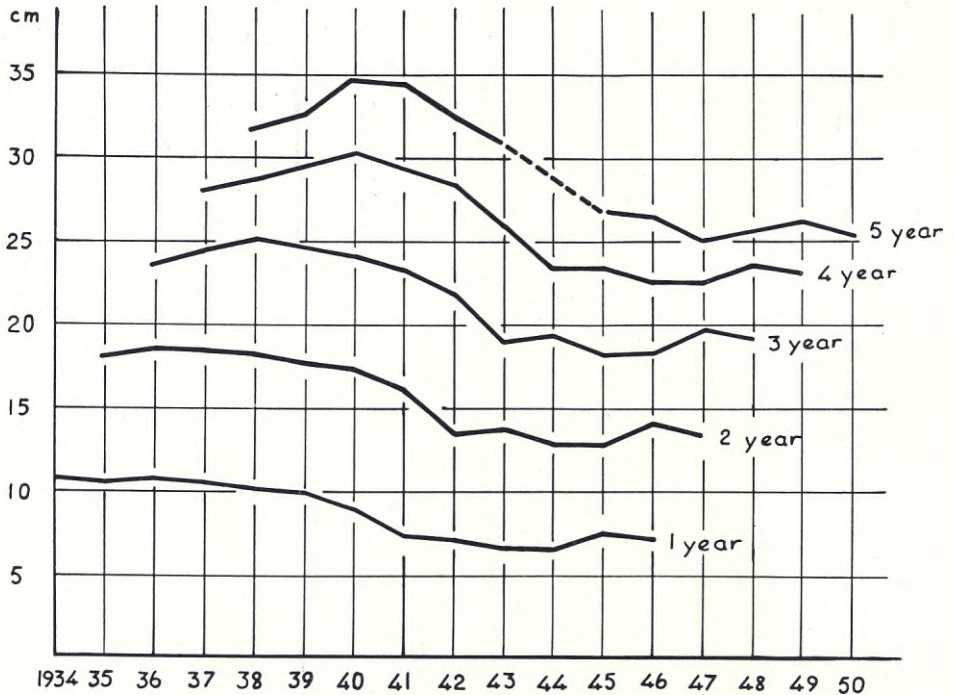


Fig. 5. Calculated mean length of char one to five years old demonstrating the changes in growth after regulation of the lake.

decrease occurs. The data do not, however, permit a comparison between the average length before the regulation and now. I have therefore, on the basis of the scales, calculated the length of the fish and Fig. 5 illustrates the calculated average length at the age of 1—5 years during different years. In that way data have been obtained from before the regulation too. We find that the growth rate of the older fish increased during the first few years after the regulation, as has been mentioned above, and after that a great decrease occurs. The average length of the char 1—3 years old, the length of which we know also before 1937, is now considerably smaller than was the case immediately before the regulation. Since the regulation there have obviously occurred disturbances in the relation between the size of the stock of fish and the supply of food in the lake.

The change in the growth rate of the char has also been accompanied by a change in the average age of the fish caught, as appears in Fig. 6. The stock of spawning char consists chiefly of three age groups, *viz* fish 3, 4 and 5 years old. During the first few years after the regulation the 4-year-old fish are predominant in the yields, but from 1943 the 5-year-old fish predominate. That is due to the selectivity of the gill-nets. Spawning char in Lake Torrön are caught in gill-nets with mesh sizes of 65 and 60 mm stretched

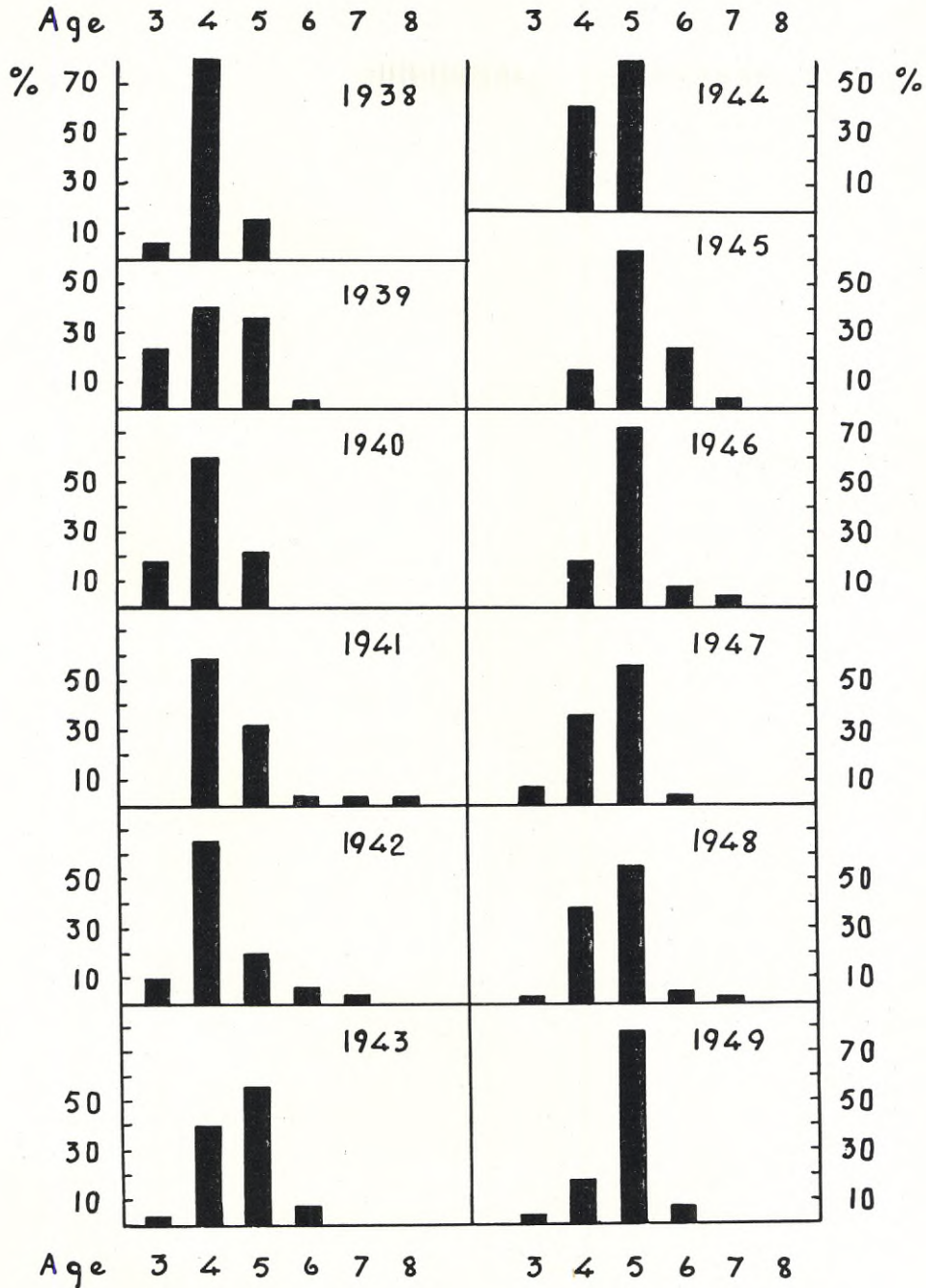


Fig. 6. Age composition of the spawning population of char during the period 1938—1949.

Table 2. Spawning fishing: catch per net (number of fish).

Year	mesh sizes mm						
	85	75	65	60	55	50	45
1939	5.6	5.6	6.3	4.7	4.2	—	—
1949	0	1.5	1.7	5.4	11.6	14.3	12.3

measure and the latter mesh size is the finest legal one according to the fishery regulation act for this province. On account of the decreased growth rate of the char, chiefly the older age groups of the spawning stock are now caught, and the fishery regulation act has prevented the net size being suited to the present size of the fish. This is clearly demonstrated by some fishing experiments carried out by the Institute in 1939 and 1949 (Table 2) with nets of different mesh sizes, among them also illegal fine-meshed nets. The table shows that in 1939, when the growth rate of the char was good, the best catches were made with a mesh size of 65 mm, whereas illegal nets with a mesh size of 50 mm secured the best catches in 1949. Fig. 7 shows, too, that in 1949 we had to use net sizes of 45–55 mm in order to get the same age composition in the catches as during the period 1938–1942 (cf Table 2), whereas the legal net sizes of 60–65 mm, which are generally used, chiefly catch the older spawning fish. This implies that the fishing of the spawning stock is nowadays less effective, which causes an increased competition in the younger age groups and thus an increased lowering of the growth rate.

Consequently, we have established that during the first few years after the regulation the growth rate of the char increased and that the spawning char that were caught had a low average age. Later, the growth rate has decreased considerably at the same time as the average age of the fish has increased. This is the same phenomenon as MILLER (1947) found in different intensities of fishing on whitefish populations. As to the char population of Lake Torrön, a change in the fishing intensity cannot very well be the primary reason, as the fishermen's journals show that during these years the fishing has been carried out with about the same number of nets and during the same number of days. The decisive factor is rather to be found in changes in the production of fish food in the lake caused by the regulation.

As DAHL (1933) has established in the Norwegian regulated lakes, there is a rich flourishing during the first few years after the damming-up, of half-pelagian and pelagian *Cladocera*, among others *Eurycerus*. Later, however, HUITFELT-KAAS (1935) proved that this flourishing was of short duration. Also in Lake Torrön we established a strong production of *Eurycerus* and plankton *Cladocera* on the shores during the first few years after the

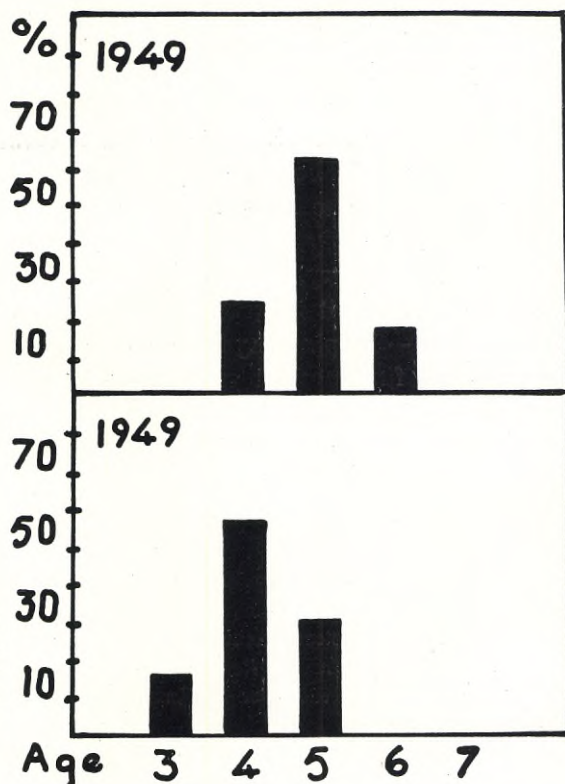


Fig. 7. Age composition of the spawning char in catches from gill nets of different mesh sizes in September 1949. Mesh sizes 60—65 mm above, 45—55 mm below.

damming-up. A large number of fish also gathered on the dammed-up bottoms and examinations of their stomach contents showed that, besides *Eurycercus* they also, to a large extent, fed on terrestrial insects and worms. After the shores had been eroded this additional supply of food disappeared in a few years. The increased growth rate of the char during the first few years after the regulation will probably be fully explained by this accessory food supply.

Fig. 5 shows that only the fish 3—5 years old show an increased growth rate, whereas the char that are 1 and 2 years old show no such increase. This will be explained by the fact that the young and the old age groups live at different places and feed on different organisms. The young fish chiefly feed on plankton and are seldom caught near the shore even in fine-meshed nets. It is chiefly the old fish that have gone on to the dammed-up bottoms and fed on the rich fauna.

When the rich additional supply of food had disappeared after a few years, the lowering of the water-level also was put into effect. By the winter draining the vegetation disappeared and performed censuses on some soft bottoms show that an impoverishment of the bottom fauna within this area has occurred. This evidently caused such a great decrease in the food supply that a decrease

in the growth rate of the char ensued. As it has not been possible to suit the mesh size to the reduced size of the fish, the fishing has grown less effective, which has secondarily contributed to decreasing the growth rate. Thus, we are faced with the risk of a future stock of dwarf char in Lake Torrön, which will be of no commercial value.

Consequently, the investigations have shown that the regulation has not — as was previously feared — caused a great decimation of the char population; on the contrary, the population has grown too big for the changed food conditions. Thus, it is wrong to try to remedy the damage — as has been done so far — by planting fry, which will only make matters worse. Instead, the use of fine-meshed nets should be allowed and fishing should be intensified so that a maximum growth rate and fish of good commercial size may be obtained.

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The Coregonid Problem. III. Whitefish from the Baltic, successfully introduced into Fresh Waters in the North of Sweden

By GUNNAR SVÄRDSON

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1. Introduction

In the last ten to fifteen years repeated plantings have been made in several lakes in the north of Sweden of fry of such whitefish as spawn in the river mouths in the Northern Baltic. The main reasons for this have been purely practical ones, for at these river mouths it has been comparatively easy to obtain a great quantity of whitefish spawn, whereas it has proved to be considerably harder and more expensive to get great quantities of it in the lakes. Another reason why fry of whitefish living in the sea have been used is that on the coast the spawning occurs in the middle of October, whereas in the lakes the majority of whitefish populations spawn later, often at the time of the freezing over, which, of course, makes the fishing of spawning

whitefish much more difficult. In the Province of Norrbotten the planting has been done by the fishery inspector E. MATTSON, and south of it, in the Province of Västerbotten, by the fishery inspector H. H. PETERSON.

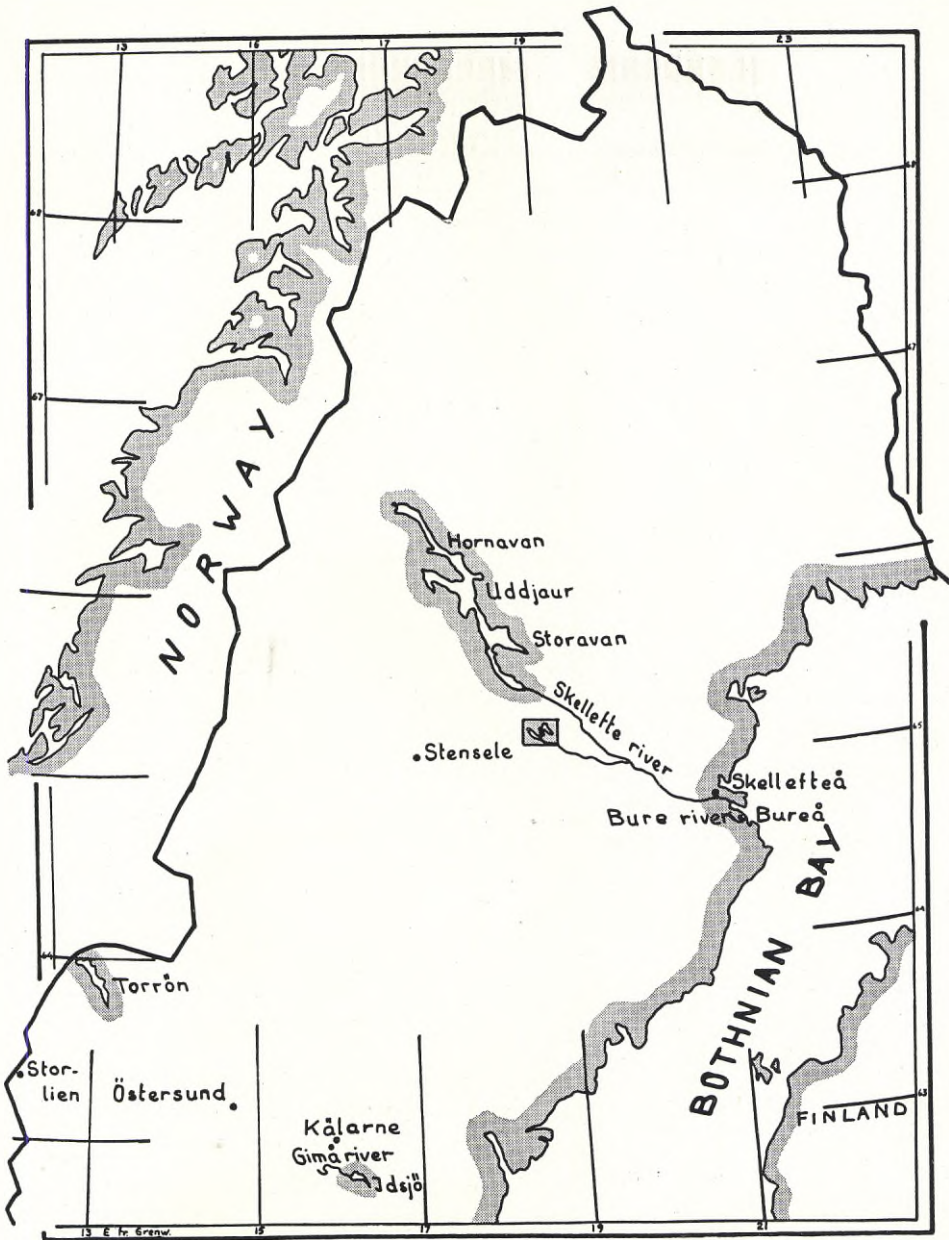
In several cases these plantings of sea whitefish into fresh water have yielded visible results in that new whitefish populations have grown up. In other cases, however, the results have not been quite so good. Experience has shown that most of the very successful plantings were in lakes where there were few whitefish before, whereas in lakes with numerous whitefish the results were, on the average, poorer. In connection with these plantings, which had a purely practical aim, we have obtained various results of great theoretical interest with regard to the coregonid problem. In collaboration with the fishery officials mentioned above I have endeavoured to make use of the results also for more principal studies of the morphological stability of the whitefish, their varying growth, conditions of spawning, etc.

The transplantations of sea whitefish dealt with in this paper concern lakes in the parish of Malå in Västerbotten, where Mr. PETERSON has been active, and he has tried to help me in every way, both in collecting material and information about the particulars of the experiments. At that time Mr. SIGVARD STENLUND lived near Lake Brunträsket in Malå, where the most important results have so far been gained, and his great interest in the whitefish and their problems has helped to throw light on several obscure points. To these two gentlemen I should therefore like to tender my sincere thanks for their most valuable cooperation.

Thanks to a lucky chance some of the scale-samples, which dr. OSSIAN OLOFSSON secured from Malå in 1927 and 1931 have been saved up to this day. But heads of whitefish, taken at the same time are now lost. I have had to my disposal a copy of Dr. OLOFSSON's notes from his Malå-visits. In 1913 dr. NILS ROSÉN preserved some specimens of whitefish in Malå, which were later donated to the Museum of Natural History of Gothenburg. Professor ORVAR NYBELIN, the present director of the museum, was kind enough to lend me this valuable material. To Messrs. OLOFSSON and NYBELIN the writer is obliged for their contribution to the information available about the whitefish species in the parish of Malå.

2. The Bure River Whitefish

There are several rivers which run out into the Baltic close to the town of Skellefteå (Map 1). At one time river spawning whitefish, sometimes in large numbers, went up these rivers in the autumn, but nowadays these whitefish populations have decreased considerably and it is actually only in the Bure River that a large number of whitefish may still be caught in autumn (PETERSON 1949). The first migrating specimens can appear as early as August, and these, who are called »leaf whitefish» (*lövsik*), move a good two



Map 1. Northern Sweden and some of the localities and lakes mentioned in the paper. The location of the Malå lakes (details on map 2) is indicated by the small rectangle near Stensele.

Table 1. Growth rate of *älv sik* in Bure River, females. Sample 1948.

Age group	Number examined	Average total length in millimetres																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
VI	5	119	192	264	338	387	416	—	—	—	—	—	—	—	—	—	—	—
VII	9	114	185	234	294	348	384	402	—	—	—	—	—	—	—	—	—	—
VIII	10	123	188	247	300	341	384	409	426	—	—	—	—	—	—	—	—	—
IX	11	123	176	226	285	326	370	406	426	443	—	—	—	—	—	—	—	—
X	8	120	183	240	281	323	354	393	428	451	469	—	—	—	—	—	—	—
XI	2	125	170	228	285	315	355	380	405	425	445	460	—	—	—	—	—	—
XII	1	145	220	280	325	365	425	440	455	490	510	530	545	—	—	—	—	—
XIII	3	122	178	217	265	298	342	375	392	422	445	468	490	503	—	—	—	—
XVI	1	120	170	220	265	300	335	360	390	430	450	480	515	555	570	585	600	—
Grand average	} (50 fish)	121	183	238	293	337	376	400	422	443	462	477	506	516	570	585	600	—

kilometres up the river before they are stopped by a dam. In the still water below this dam they then remain until the spawning time in October. In addition, there is a much frequented spawning place exactly at the outlet of the river into the sea, and here the whitefish begin to appear at the end of September, the spawning reaching its peak in the middle of October. At this spawning place the spawning occurs in the evening, between about 5 and 12 p.m., and is most intensive about 9 to 11 p.m. The whitefish seem to spend the rest of the day in a bay outside the river mouth. According to the fishermen, the males are in the habit not only of arriving first in the season but also first every day the whitefish meet to spawn. The spawning chiefly takes place on a bottom with big stones and at a depth of about a half to one and a half metres. On a visit to the spawning place in October 1948 I could establish that the water temperature was then 2.8° Centigrade.

Of old, the whitefish are caught in nets which are pulled with the stream close to the bottom. They are hardly one metre in diameter and are provided with handles 5—6 m long. The hauls of one evening can yield up to 300 fish and the average weight is about 1 kg or slightly less.

The Bure whitefish belongs to the same species of whitefish as is to be found along the whole Swedish Baltic coast. It has a fairly long snout, has a fair number of gillrakers, about 25—34 with an average of 28 or 29, and can migrate along the coast. It is the same species of whitefish as has been studied by DAHR (1947) and JÄRVI (1928), but it is, at present, not quite certain that the whitefish studied by ROSÉN (1920) belonged to this species only, although it was certainly represented among his material.

A sample of the whitefish spawning at the mouth of the Bure River taken on October 16, 1948, was sent down to the Institute at Drottningholm and

Table 2. Growth rate of *älvsik* in Bure River, males. Sample 1948.

Age group	Number examined	Average total length in millimetres											
		1	2	3	4	5	6	7	8	9	10	11	12
V	3	137	218	297	337	362	—	—	—	—	—	—	—
VI	10	134	196	257	321	364	382	—	—	—	—	—	—
VII	11	120	183	231	270	313	345	365	—	—	—	—	—
VIII	12	117	186	239	284	318	350	373	389	—	—	—	—
IX	6	112	181	218	251	282	317	345	363	383	—	—	—
X	3	110	170	197	225	263	300	342	373	392	410	—	—
XI	1	95	135	170	235	280	320	335	370	395	410	420	—
XII	2	105	143	180	213	268	298	318	360	378	398	413	433
Grand average (48 fish)		121	185	236	280	319	345	359	378	385	406	415	433

was then studied there. The sample comprised 50 females and 48 males, which except for sex, were taken at random.

The growth of the Bure whitefish has been studied on the basis of the scales, the same method being used as before (SVÄRDSON 1950), this entailing the use of EINSELE's (1943) relation curve between the size of the scale and the length of the fish body. Table 1 shows the growth of the females and Table 2 that of the males. The growth is somewhat poorer than that found by DAHR (1947) in the same species of whitefish on the coast of Upland, which is only natural seeing that the length of the growth period is shorter in the northern than in the middle part of the Baltic. ROSÉN's (1920) growth figures for whitefish, from approximately the same district as that of the Bure whitefish, are not comparable as he used the old direct proportional method in his calculations on the scales, which gives far too low values of the growth during the first few years. The same thing applies to ALM's data (1917) on the growth of whitefish in Hjälmarén. JÄRVI's (1928) data on the growth of the whitefish on the Finnish Baltic coast seem to indicate a better growth there.

DAHR (op.cit.) found that on the coast of Upland the male and female whitefish displayed the same rate of growth, although the females were predominant among the big whitefish. DAHR views this as a result of the males being more exploited by fishing. Tables 1 and 2 show, however, that in the case of the Bure whitefish the growth of males and females is the same during the first three years, but after that time the growth of the males becomes proportionately slower. There are, it is true, no four-year-old spawning males in the sample from the mouth of the Bure River, but this is probably due to the large mesh-size of the nets used. If we suppose that sexual maturity occurs at the end of the fourth growth period, the decrease in the growth of the males as compared to that of the females is satisfactorily

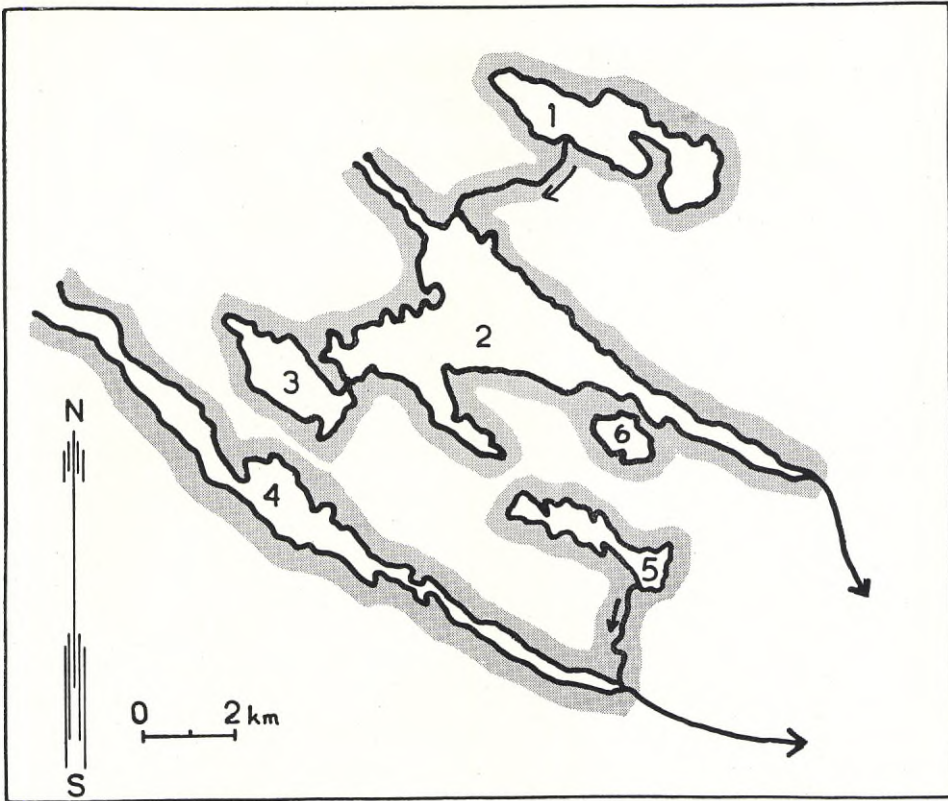
explained. DAHR's view that the growth of the two sexes is similar is contradicted by VAN OOSTEN and HILE (1949), who found that the female whitefish in Lake Erie grew better than the males; but DAHR's view may nevertheless be correct, for a slower growth of the males need not be of a hormonal origin and directly affect the metabolism, but may very well be due to the fact that the males gather earlier at the spawning places and their effective growth period consequently becoming somewhat shorter. If the spawning occurs early in autumn — there is a difference of about one month between the Bure area and the coast of Upland — this shortening of the growth period may be of greater importance farther north than south, where the growth at this time of the autumn should be small anyhow. This is true provided that the whitefish has an inner annual rhythm of growth similar to that of *Salmo trutta* as proved by BROWN (1946).

As the number of gillrakers may most easily be supposed to change by selection, so that specimens with an extreme number of gillrakers may normally grow more slowly than those with the »ideal» number, I have — with a view to testing the method — studied the relation between growth and the number of gillrakers in the specimens from the Bure River. The »ideal» number of gillrakers in this environment was then supposed to be the average value of the population, which, with a margin on both sides, was put at 27, 28 or 29 gillrakers on the first gillarch. All the other figures — both higher and lower than this optimum value — were then listed in a group to be compared with the first group. This second group comprised specimens with 24—26 or 30—33 gillrakers. The growth (in millimetres) of the two groups was, however, almost identical, as appears from the following list:

	year 1	year 2	year 3	year 4	year 5	year 6
Gillrakers 27—29, males (25)	121	187	236	280	319	347
» 24—26, 30—33, males (23) . . .	120	183	234	280	318	342
» 27—29, females (19)	122	182	232	292	334	376
» 24—26, 30—33 females (31) ..	120	184	242	294	338	375

There need only be some difference in growth between two such groups for a selection to be formed, for the growth affects the time at which the first sexual maturity occurs and thus the number of generations. In the case of the Bure whitefish, however, the growth seems to be the same, irrespective of the divergencies between the specimens as to the number of gillrakers on the first gillarch. This may indicate that under the present environmental conditions no concentration towards the present average number of gillrakers occurs in this whitefish population.

If no selection occurs — the frequency of possible mutations is of course quite unknown — the number of gillrakers and the variation of this number should be constant. The variation scope is fairly large in all whitefish popula-



Map 2. The Malå lakes. 1 Lajnjaure, 2 Stora Skeppträsket, 3 Lilla Skeppträsket, 4 Malå River, 5 Brunträsket, 6 Kälingträsk.

tions — it often comprises 10 units — and is in itself probably an adaption to quick changes, should such be necessary, in accordance with the principle of balanced polygenes (cf. MATHER 1942, SVÄRDSON 1944).

The morphology of the Bure whitefish and, particularly, its constancy at different growth rates will be discussed in detail in another section where we shall discuss the *älv sik* in fresh water within the parish of Malå.

3. The two Whitefish Species in the Lakes in the Malå District

The big parish of Malå is situated about 120 kilometres northwest of the town of Skellefteå and 310—340 metres above the sea (see Map 1). It contains several lakes, some of which we shall discuss more closely, namely Lajnjaure, Stora Skeppträsket, Lilla Skeppträsket, Kälingträsk, Brunträsket, and the River Malå with its lake-like portions (see Map 2).

All the lakes are of the oligotrophic type with fairly bare, stony shores.

Table 3. Growth rate of *storsik* in Lake Brunträsket, sample 1927.

Age group	Number examined	Average total length in millimetres						
		1	2	3	4	5	6	7
III	3	146	207	228	—	—	—	—
IV	12	140	195	223	239	—	—	—
V	10	135	192	220	241	256	—	—
VI	5	143	188	211	229	253	273	—
VII	4	138	184	211	236	253	266	276
Grand average	(34 fish)	139	193	219	237	254	270	276

Besides whitefish, there are perch, burbot, pike, and stray trout. Whitefish has always been the economically most important species of fish (PETERSON 1949, STENLUND 1947).

Two species of whitefish are probably original in these lakes. One of them, the *storsik*, existed in all the lakes until quite recently, with the possible exception of the River Malå. In Lajnijaur it was large-sized, in the other lakes smaller. According to old statements preserved by oral tradition, this whitefish was transferred by the Laplanders to Brunträsket from Lilla Skeppträsket, and so it is perhaps not original in Brunträsket, or, if it is, it has once declined and perhaps died out. In Lajnijaur the species disappeared almost entirely about 1930, probably because of diggings in the wood near by, when a lot of mud and bog water ran out into the lake. Dead specimens embedded in the ice then indicated that they emigrated to or were washed out dead into Stora Skeppträsket, and after that time only stray, always big, whitefish were caught in Lajnijaur. In Brunträsket, too, the stock of *storsik* decimated strongly. At the time of OLOFSSON's visit in 1927 it was small-sized and thin, and the fishery regulation act was altered in that the legal mesh-sizes were made smaller. This caused temporary increase in the fishing, but the whitefish rapidly grew less numerous, the size increasing instead, and since about 1937 there were — as in Lajnijaur — only stray big whitefish, and they were so few that the fishing during the spawning time, which had earlier been very intense, was completely abandoned. Brunträsket, which was earlier regarded as the best whitefish lake in the district, was almost deserted by fishermen of whitefish. As to the occurrence of *storsik* in the other lakes there is but scanty information. In Lilla Skeppträsket fairly large numbers of this species have been caught but in Stora Skeppträsket the *storsik* population is small.

The second species, *blåsik* or *löja* as it is called by the local population has apparently always been the predominant species in Lilla and Stora Skeppträsket. Particularly in Stora Skeppträsket it is very abundant and also very small. Earlier, people fished with a seine and the *blåsik* were caught

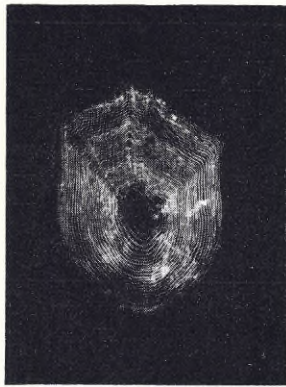
Table 4. Growth rate of *storsik* in Lake Brunträsket, samples 1948—1950.

Age group	Number examined	Average total length in millimetres									
		1	2	3	4	5	6	7	8	9	10
II	1	175	255	—	—	—	—	—	—	—	—
III	4	165	259	313	—	—	—	—	—	—	—
IV	10	162	255	324	354	—	—	—	—	—	—
V	17	156	245	312	345	362	—	—	—	—	—
VI	9	161	248	308	344	363	374	—	—	—	—
VII	1	140	245	295	340	370	390	395	—	—	—
XIII	2	135	210	255	320	368	398	418	435	453	465
XIV	1	175	240	265	305	365	405	435	450	480	505
Grand average	(45 fish)	159	248	310	345	363	382	417	440	462	478

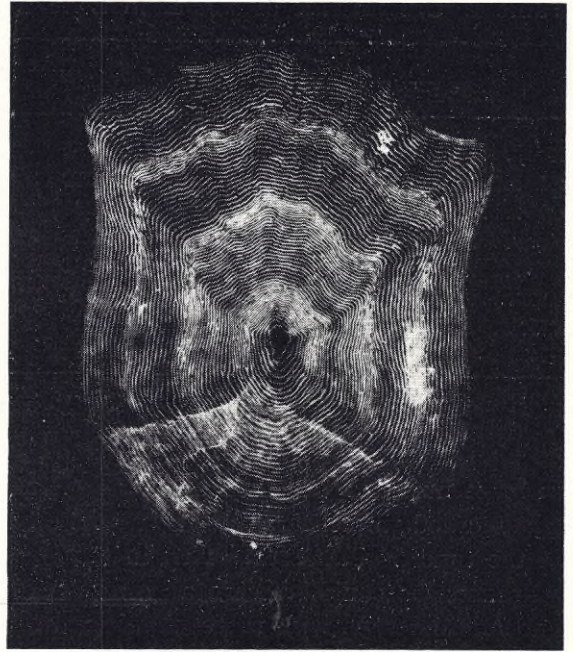
in large numbers, but then the seines went out of use and since then only fine-meshed gill-nets are used. By all appearances it still existed in Brunträsket at the time of OLOFSSON's visit in 1927 as, when counting the number of gillrakers, he could discern a type with few and short gillrakers (*storsik*), and another type with more gillrakers, which was probably *blåsik*. It does not seem to have been particularly small in Brunträsket, at that time anyhow. Now there are no *blåsik* in Brunträsket. We do not know if it has ever existed in Lajnijaur or in the River Malå.

The two species have always spawned at about the same time, that is from Christmas to about the middle of January. But the spawning places have always been different, the *storsik* having spawned at a depth of 2—4 m on fairly firm but sedimentary bottom, often covered with *Isoetes*, the *blåsik*, on the other hand, on loose bottoms at a depth of 4—7 m. On my request PETERSON and STENLUND made artificial fertilization of spawn so that both species were crossed, in the winters of 1949 and 1950. The appearance of these hybrids has not yet been studied but they have been released into tarns devoid of fish and lying in the district. The fish used in these hybridizations were *storsik* from Brunträsket and *blåsik* from Stora Skeppträsket.

The growth of the *storsik* was studied on samples taken in connection with these hybridizations in 1949 and 1950. The scale samples of the *storsik* in Brunträsket taken by OLOFSSON in 1927 have also been studied. The growth has been studied on the scales in the usual manner and will be found in Tables 3 and 4. As the tables show, an essential change in the growth of the *storsik* in Brunträsket occurred between 1927 and 1948—50. We know well from many other waters in Sweden that the growth of a whitefish might change quite considerably within one and the same lake in the course of a few decades. Even if, in some cases, this may be due to slow changes in the lake's production of food for the whitefish, it is no doubt, in most cases, due to changes in the size of the population and thus to the quantity of food



a



b

Fig. 1. Scales of two *blåsik* specimens in their fourth growth season. a) Stora Skeppträsket, 154 mm, b) Kålingträsk, 300 mm. Fish secured 1913 and preserved in the Museum of Gothenburg.

available for each individual fish. As will be discussed later, there is some evidence that the number of *storsik* in Brunträsket changed again at the same time as the Bure whitefish were transferred from the sea.

The growth of the *blåsik* in Stora Skeppträsket was studied on a scale-sample taken 1949. Moreover, OLOFSSON's sample from the year 1931 was included. Finally, the preserved specimens, mentioned in the introduction and secured by ROSÉN in 1913 were compared. These specimens are labelled »Kålingträsk, near Stora Skeppträsket, 15.8.1913» in the collections of the museum of Gothenburg. Dr. ROSÉN has kindly told me that he has no notes, nor memories on the fishing or the reason he then had to preserve the fish. However, SIGVARD STENLUND has informed that *blåsik* were formerly transferred alive from Stora Skeppträsket to the very small Kålingträsk, situated close by. It must be remembered that the plasticity of growth in whitefish has been known for centuries in northern Sweden and the inhabitants have taken profit of many small lakes by transfers of fish, which as a rule grew very rapidly the first years (until the population becomes to large). STENLUND has been told by the people of the district that the last transfer of *blåsik* from Stora Skeppträsket to Kålingträsk should have occurred »some 40 years ago».

Table 5. Growth rate of *blåsik* in Stora Skeppträsket, transferred as adults to Kålingträsk, sample 1913.

Age group	Number examined	Average total length in millimetres					
		1	2	3	4	5	6
II	19	74	105	(127)	—	—	—
III	6	78	115	138	(154)	—	—
IV	4	66	100	132	152	(166)	—
V	2	68	95	130	149	159	(171)
Grand average	(31 fish)	73	106	135	151	159	—

Table 6. Growth rate of *blåsik* in Stora Skeppträsket, sample 1931.

Age group	Number examined	Average total length in millimetres							
		1	2	3	4	5	6	7	8
III	2	70	120	158	—	—	—	—	—
IV	10	66	100	151	179	—	—	—	—
VI	7	71	104	127	150	180	196	—	—
VII	17	67	100	126	142	155	184	202	—
VIII	7	69	99	116	132	146	157	182	203
Grand average	(43 fish)	68	101	132	151	159	181	196	203

Table 7. Growth rate of *blåsik* in Stora Skeppträsket, sample 1949.

Age group	Number examined	Average total length in mm					
		1	2	3	4	5	6
III	27	77	121	150	—	—	—
IV	8	70	119	163	176	—	—
V	13	72	121	160	176	189	—
VI	2	70	120	158	183	193	205
Grand average	(50 fish)	74	121	155	177	190	205

Table 8. Growth rate of *blåsik*, born in Kålingträsk, sample 1913.

Age group	Number examined	Average total length in millimetres					
		1	2	3	4	5	6
II	1	95	176	(227)	—	—	—
III	1	95	176	245	(300)	—	—
IV	1	108	213	248	295	(336)	—
V	1	78	150	207	250	300	(326)
Grand average	(4 fish)	94	179	233	273	300	—

The scales of these museum-fish were quite clear and easily read. From them it was evident that several transfers had been undertaken. The majority of fish (31 specimens) had just been transferred, possibly actually when ROSÉN made his visit, but four of them were significantly larger with a much better growth. Their gillrakers proved them to be *blåsik* as well. They were certainly born in Kålingträsk as progeny from an earlier transfer from Stora Skeppträsket. Thus again the plasticity of whitefish growth was demonstrated (Figure 1 and Tables 5, 6, 7 and 8). Since the majority of ROSÉN's fish bear witness to the growth in Stora Skeppträsket, though they might have lived in Kålingträsk for some shorter time (less than a growth season), they have been referred to in the tables as a sample from Stora Skeppträsket.

It is seen from the tables and Figure 4 that the *blåsik* in Stora Skeppträsket had the same growth in 1913 as in 1931 but in 1949 growth had improved somewhat. Undoubtedly the population has all the time been very large and still in 1949 and 1950 the fishing of STENLUND and PETERSON gave hundreds of fish in some few gill-nets during one single night.

4. The Bure Whitefish introduced into the Lakes in the Malå District

As early as 1938 the first whitefish fry from the coast outside Bureå were planted into the Malå lakes and since 1942 only fry emanating from spawn gathered at the fishing places at the mouth of the River Burå, have been used. The quantities of fry planted up to 1947 were as follows:

Lilla Skeppträsket		Lajnijaur	
1938	370,000 fry	1942	100,000 fry
1943	60,000 »	1945	300,000 »
1944	50,000 »	1946	300,000 »
1945	?	1947	150,000 »
1946	?		
1947	50,000 »	Brunträsket	
Stora Skeppträsket		1945	100,000 »
		1946	100,000 »
1942	75,000 »	1947	100,000 »
1943	80,000 »		
1944	50,000 »		
1945	?		
1946	200,000 »		
1947	100,000 »		

In the two Skeppträsk lakes little has been noticed of the fry planted, although stray fish have been caught, believed to have been Bure whitefish, which, of course, is doubtful as the number of gillrakers, etc., has not been studied.

On the other hand, great changes in the whitefish fishing have occurred both in Lajnijaur and Brunträsket. In the autumn of 1944 people began to get big catches of spawning whitefish in Lajnijaur, and this was at quite new places where, earlier, no spawning whitefish occurred. Those who found these spawning places tried to keep their discovery a secret but, of course, the rumour soon spread round the lake, and in the autumn of 1948 about thirty families took part in the fishing of spawning whitefish which was then carried out at various places around the lake and was the general topic of conversation in the neighbourhood. On the best nights the quantity of fish caught was as much as 500 kg and during the season of 1948 a total of about 4,000 kg of whitefish was caught in Lajnijaur, where in the years prior to the plantations of fry only stray specimens of whitefish had been caught. What was most remarkable was, the fishermen thought, that although no whitefish had ever spawned in that district at any other time than between Christmas and early January, this new whitefish species spawned as early as the middle of October and in shallower water than the old, extinct whitefish. The introduced Bure whitefish spawned at points and shoals at a depth of between 0.5 and 1.5 m on coarse gravel and over big stones, that is at the same depth and on the same kind of bottom as in their home locality in the River Bure. But, as far as we know, they did not go down into the outlet from Lajnijaur, that is into running water, which was considered to be such an important character of the Bure whitefish. For whitefish spawning in running water is called, along the whole coast of northern Sweden, *strömsik* or *älvsik*, that is »river whitefish».

The release of Bure whitefish fry in Brunträsket was considered by many people to have small chances of success, as there were a large number of perch (*Perca fluviatilis*) in the lake and consequently small individuals. At the time when the whitefish population in Brunträsket was large, there were also perch, but then they were large-sized and by all appearances far less numerous. The numerous small-sized perch which existed in Brunträsket in 1945 were now regarded as a potential enemy of the whitefish fry, which were consequently not believed to be able to survive in large numbers.

But these fears proved groundless; on the contrary, the plantation was a great success and as early as the latter part of the summer of 1946 they caught in the lake several twosummer-old whitefish, belonging to year-class 1945, and showing a very good growth, thus probably being Bure whitefish. That was confirmed in the autumn of 1947 when the first sexually mature specimens were found, at places where no whitefish had spawned before and as early as October, which had never happened before in the lake. Fishing during spawning time was prohibited in Brunträsket by the local fishery association, but in the middle of October 1948 the present writer was there in the company of HANS PETERSON and SIGVARD STENLUND, and about sixty spawning whitefish were then caught at the places that had

Table 9. Growth rate of *älsik* in Lajnijaur, sample 1948.

Age group	Number examined	Average total length in millimetres										
		1	2	3	4	5	6	7	8	9	10	11
VI	5	117	203	283	351	415	463	—	—	—	—	—
VII	5	117	196	258	315	367	415	445	—	—	—	—
VIII	14	108	172	235	278	338	381	421	448	—	—	—
XI	8	109	168	218	266	305	336	366	395	417	437	456
Grand average	(32 fish)	111	180	242	292	346	388	409	429	—	—	—

earlier been located by STENLUND who was then living at the lake. The spawning occurred on a bottom of big stones, *i.a.* at a place near the shore where big stones had been dumped. In 1949 and 1950 only three or four very small spawning places were found in Brunträsket, all of them on bottoms with big stones and at a depth of 0.5 to 1.5 m. The old native *storsik*, on the other hand, spawns at a greater depth and at many more places round the lake.

According to STENLUND the perch showed, as early as 1949 and 1950, a marked tendency to decrease in number and increase in average size. If possible, we shall follow this tendency in the future to see whether the perch become large again, which is quite feasible, as TÄGTSTRÖM (1937) has established that the young whitefish feed on the pelagic stage of the perch fry. Thus, in this case at least, the whitefish would seem to be the stronger of the two species.

The two samples of spawning Bure whitefish, taken in October 1948 in Lajnijaur and Brunträsket, respectively, were sent down to the Institute at Drottningholm, where they have later been studied. In both cases a first examination gave interesting results. As we know, the first plantation in Lajnijaur was made as early as 1942, and consequently, no whitefish older than seven summers should occur among those netted in the autumn of 1948. And yet that was the case (see Table 9), and a number of them were 11 years old, but nevertheless without any doubt Bure whitefish. Since no other plantation has been made except the one in Lilla Skeppträsket in 1938, the specimens apparently originated from that plantation, which left no traces in Lilla Skeppträsket, as far as we know. The Bure whitefish must then have migrated through Stora Skeppträsket and up into Lajnijaur (see Map 2); probably this happened in their first extensive spawning, in 1941. Thus, they have turned out to be, to some extent, migratory, though nothing of the kind has been observed in Lajnijaur. After their first natural spawning in Lajnijaur in 1941 they seem to have survived very well and given rise to a large population. Consequently, it is uncertain whether the plantations of fry in Lajnijaur itself, beginning in 1942, affected the population at all. It

may very well be and that is actually the most probable explanation — that it was the plantation in Lilla Skeppträsket in 1938 that caused the rich whitefish fishing in Lajnijaur in the nineteen-forties. As a result of the rich fishing the people living round the lake have become quite convinced that all plantations are profitable. So plantations have been continued during the last few years, too, although the fishery experts warned and advised against them, pointing out that they would probably give no results at all, or, if they really were successful, would cause the whitefish population in Lajnijaur to become too large, this resulting in a poorer growth rate. Thus, the rich whitefish population in Lajnijaur is not, as the inhabitants believe, definitely the result of the plantations made there, but probably the result of one single plantation in quite another lake!

5. The Problem of Obtaining Pure Samples of Whitefish

Everyone who has studied whitefish more closely in Europe — where two species of whitefish often exist in the same lake — has made the experience that a sample is often not entirely pure but contains foreign specimens, too. At the spawning places they appear, above all, as spawn-feeders, possibly stimulated, too, by the schooling behaviour of whitefish. The importance of this problem has been pointed out before by SVÄRDSON (1949), and JÄRVI (1928) had several cases where specimens of a foreign species were contained in one single sample. This problem is of great importance for the study of the morphological characters of different whitefish species, and from the literature on this matter it is easy to see that the variation of the number of gillrakers, for instance, is often so great that it actually indicates that more than one species occurs among the fish examined. If one disregards this, and uses the enlarged variation figures as a measure of how one single species of whitefish »varies», it is no wonder that many grossly erroneous interpretations arise. DOTRENS and QUARTIER (1949) have shown how the variation in the sympatric species of *C. macrophthalmus* NÜSSLIN and *C. exiguus* KLUSINGER in Lake Neuchatel overlaps in regard to all important morphological characters. They have managed to distinguish the two species but it is apparent from their figures how easily a mistake may have arisen in a case where one single species had been believed to vary. If we compare STEINMANN's (1950) and DOTRENS' (1950) descriptions of the whitefish in Lac Lemon we realise how easily mistakes arise as a result of the samples not being pure. According to DOTRENS (1950), KREITMANN's (1929) often quoted statement on the drastic change in the number of gillrakers in a whitefish as a pure environmental modification, was caused by a confusion. Without any doubt there are many similar cases, on a smaller scale, in all such samples as have been taken outside the spawning time, when, of course, a mixing up of two sympatric species is still easier than during spawning time.

Table 10. Growth rate of *älvsik* in Brunträsket, sample 1948.

Age group	Number examined	Average total length in millimetres			
		1	2	3	4
IV	50	167	279	341	371
Grand average	(50 fish)	167	279	341	371

Since the first plantation of *älvsik* was made in Brunträsket in 1945 and the fish studied were caught in October 1948 when they had finished their summer growth, the scales should disclose four summer zones. That was also the case in all but one fish, which was five summers old, and which therefore must be a *storsik* of the old native stock. That clearly proved that the sample was not quite pure, although other *storsik* — if there were any others in that catch — must have been hatched in 1945, which seemed little probable in view of the well-known low frequency of the species in the lake. But the distribution of the gillrakers was suspect:

Number of gillrakers	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Bure River	—	—	—	—	—	1	6	15	11	17	16	13	12	6	1	—
Lajnijaur	—	—	—	—	1	—	2	1	2	4	5	5	3	5	1	3
Brunträsket	1	—	—	2	2	2	2	3	4	12	4	8	9	3	7	—

Since the *storsik* has a smaller number of gillrakers than the *älvsik*, the small numbers in some specimens contained in the sample from Brunträsket seemed very suspect. This impression was also strengthened by the fact that several of these specimens with a small number of gillrakers also had *Daphnia* in their stomachs, whereas all the others had only remnants of spawn or *Trichoptera*, which, according to STENLUND's investigation of stomach contents, had formed the staple food of the *älvsik* in Brunträsket. A closer investigation of the suspected specimens disclosed, too, that they differed in some morphological characters, yet not so much that they could be sorted out because of any one such character. According to an analysis of the scale samples from the spawnings of 1949 and 1950, the growth of the *storsik* was somewhat poorer than that of the *älvsik*, although very inconsiderably so (Table 10), and so also this quality might — in this special case — be of a certain diagnostic value. We therefore tried to take into consideration several of these different characters at the same time, sorting out the suspected specimens, which were no less than nine. This was done by giving each of the 59 specimens studied »points» for a number of different characters, and then the presumed *storsik* ought to get comparatively low points every time and consequently a low total »score».

Number of gillrakers on the first arch

	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
<i>Älvsik</i>	—	—	—	—	—	1	1	2	4	11	4	8	9	3	7
<i>Storsik</i>	1	—	—	2	2	1	1	1	—	1	—	—	—	—	—

Longest gillraker in mm/length of gill-arch in mm

	0.120—124	0.125—129	0.130—134	0.135—139	0.140—144	0.145—149
<i>Älvsik</i>	—	2	1	2	3	4
<i>Storsik</i>	2	2	2	2	1	—
	0.150—154	0.155—159	0.160—164	0.165—169	0.170—174	0.175—179
<i>Älvsik</i>	6	7	4	6	2	2
<i>Storsik</i>	—	—	—	—	—	—
	0.180—184	0.185—189	0.190—194	0.195—199	0.200—204	
<i>Älvsik</i>	4	2	2	2	2	
<i>Storsik</i>	—	—	—	—	—	

In this way each specimen was awarded points according to its qualities, and the lowest group (*e.g.* 91 scales or 19 gillrakers) was given the figure 1, the next group the figure 2, etc. Thus each specimen was given a score, which for the *storsik* was between 19 and 41, but higher for the *älvsik*, between 44 and 101. Since a rapidly grown fish automatically obtained a higher score because of greater body length and greater length and height of snout and bigger eye, this source of error had to be considered, too, and this was done by calculating straight regression lines for the relation between body size and score (Fig. 2). Then it became quite clear that the nine suspected specimens really differed from the others, so that it was justifiable to classify them as *storsik*. Out of the nine specimens 8 were males, and 6 had plankton in their stomachs.

This unexpected element in the catch of *älvsik* thus showed that the *storsik* was not so scantily represented in Brunträsket as had been supposed before. In 1949 and 1950 special efforts were therefore made to catch *storsik* during its spawning time, and then the fish shown in Table 4 were obtained. In the three samples taken from Brunträsket, the various year-classes are represented by the following number of specimens

	Born 1948	1947	1946	1945	1944	1943	1942	before 1941
Catch 1948 (9+1 specimens)	—	—	—	9	1	—	—	—
» 1949 (19 specimens) ..	1	4	—	8	3	—	—	3
» 1950 (16 specimens) ..	—	1	8	6	1	—	—	—
Total number of fish caught	1	5	8	23	5	—	—	3

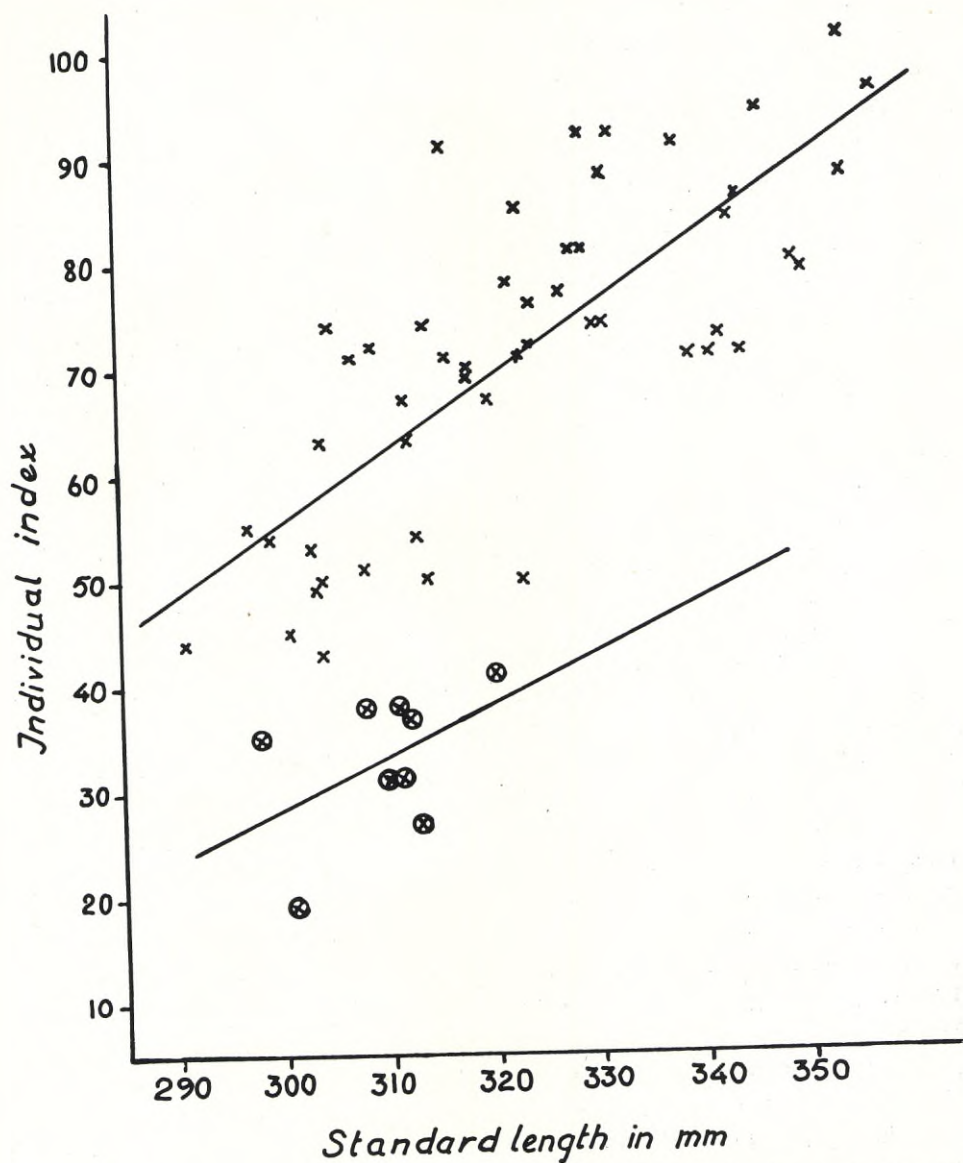


Fig. 2. In order to separate the *storsik* from the *älvsik*, caught at the same time, a system of individual index was used (see text). As the index was correlated with size, regression-lines must be used to demonstrate the lower index of the nine *storsik* specimens.

This material is small, but it seems to indicate that the *storsik* of year-class 1945 in Brunträsket were unusually numerous. This is of great interest as it was that very year that the Bure whitefish were planted and the planting proved so successful. According to PETERSON'S (1949) calculations, about

10 per cent of the Bure fry planted were recaptured in Brunträsket up to and including 1948, which indicates an extremely high percentage of survival compared to normal conditions. In 1948 the yield of the new whitefish fishing was about 12 kg per hectare as compared with about 7 kg in Lajnijaur. This alone seems to indicate that considerable numbers of the native *storsik* must have been caught in Brunträsket in 1948, though nobody believed it at that time, especially as all the whitefish caught appeared to have been born in 1945, *i.e.* the year of the plantation of the Bure whitefish. The *storsik* population must have increased almost explosively, which implies that the old population, before 1945, must have been sparse.

6. The Effect of Hot Summers on Whitefish Populations

The sudden increase in the native *storsik* population of Brunträsket in 1945 may be due to two different reasons:

1. The plantation of *älsik* favoured the *storsik* population.
2. The year 1945 was favourable, resulting in a good year-class of *storsik* and causing the *älsik* transplanted from Bureå to survive, too, to an unusually large extent.

The first explanation is improbable for, as has been mentioned above, it is a common experience that the plantation of whitefish generally is far less successful in lakes where there already lives a whitefish population than in lakes where there are no whitefish before. The most probable influence of one whitefish population on another is, of course, that a competition for food ensues, since, as far as we know, all species of whitefish feed on plankton during their first summer.

Thus, *a priori*, the second explanation seems more probable, that is that in the summer of 1945 conditions were favourable to the survival of the whitefish fry and so gave rise to rich year-classes. The whitefish population of the river Gimå in Jämtland, which has been studied during the last few years by TOOTS, had an unusually rich 1945 year-class, which increased later catches from 4,000 up to 29,000 fish (TOOTS 1949, RUNNSTRÖM 1950, p. 12, and TOOTS, unpublished). With regard to char (*Salmo alpinus*) RUNNSTRÖM (1951) has found that in Lake Torrön in Jämtland the 1945 year-class also was very rich. This fact alone, *i.e.* that in two different water systems besides Brunträsket, the 1945 year-classes were unusually rich ones, points to a climatic factor being responsible for the change.

Therefore, temperature data from official meteorological reports have been compared for three places in the north of Sweden (Tables 11 and 12). They disclose that in 1947 and 1945 summer temperatures were considerably higher than normal, particularly in 1947. 1945 was also exceptionally hot, though June was more normal than July and August, whereas in 1947 all

Table 11. Summer temperature (centigrade) 1930 and 1942—1949 in northern Sweden.

Locality	Month	1930	1942	1943	1944	1945	1946	1947	1948	1949	Mean 1901—30
Stensele	June . . .	12.6	9.6	12.6	9.1	11.2	10.6	13.7	10.3	11.1	10.8
	July . . .	16.5	13.1	13.9	14.0	15.6	15.0	15.6	14.3	12.4	14.0
	August . .	14.2	12.0	11.1	12.1	13.8	12.5	13.2	10.5	10.8	11.4
Östersund	June . . .	13.7	10.4	12.7	9.8	11.9	11.0	14.6	11.9	11.5	11.3
	July . . .	16.3	13.4	13.8	15.2	16.1	15.5	15.9	16.2	13.3	14.2
	August . .	14.9	13.4	11.6	13.5	14.5	13.2	15.2	11.6	12.1	12.2
Storlien	June . . .	11.3	7.3	9.4	7.0	9.1	8.6	11.2	8.2	8.2	8.0
	July . . .	13.3	10.0	11.1	12.6	13.4	13.0	12.5	13.2	9.6	11.2
	August . .	12.6	10.8	8.9	10.8	11.9	11.0	12.0	8.7	9.2	9.7

three summer months were extremely hot. The growth of the whitefish in the north of Sweden is in the main restricted to these three months, and the whitefish fry are probably hatched towards the end of April or during May.

It has previously been established in Sweden that hot summers have had an effect on whitefish populations. In his routine studies of whitefish scale samples from the north of Sweden, OLOFSSON (1932) found that in many lakes the very hot summer of 1930 caused a very strong growth, which was reflected in broad growth zones on the scales, whereas on the other hand, the following summer, 1931, which was unusually cold, resulted in a poor growth and very thin growth zones, in some exceptional cases even no visible growth zone at all. VALLIN, who has for many years studied the regulation of Lake Suorva and its effect on the fish population, has in an unpublished manuscript which I have had an opportunity of reading, given an account of the frequency of bottom animals in Suorva for the years 1927, 1928, 1929, 1930, and 1933. It was then found that in August, on an area of one square metre in the litoral zone, there were in each of those years 77, 87, 129, 361, and 147 specimens of *Chironomidae* larvae. This would seem to prove a strongly increased production in the litoral zone in 1930, and as the water temperature was much higher than normal, the plankton production was most probably higher than normal, too, though unfortunately there are no samples to prove it. The hypothesis that the high temperature was responsible for the higher production in 1930 in Suorva is also supported by the fact that below the metalimnion, at a depth of 10—21 m, the number of bottom animals was almost constant during the five years studied.

Since the summer growth in 1930 could be studied in the scale-sample from Stora Skeppträsket taken by OLOFSSON in 1931 the statements by

Table 12. Mean temperature (centigrade) for the period June—August 1930 and 1942—1949.

Locality	1930	1942	1943	1944	1945	1946	1947	1948	1949	Mean 1901—30
Stensele	14.5	11.6	12.5	11.8	13.6	12.7	14.2	11.7	11.4	12.1
Östersund	15.0	12.4	12.7	12.9	14.2	13.3	15.2	13.2	12.3	12.6
Storlien	12.4	9.4	9.8	10.2	11.5	10.9	11.8	10.1	9.0	9.7

OLOFSSON could be verified by the present writer. The growth reaction of the different year-classes in this lake on the summers 1930 and 1947 has been illustrated in Figure 3.

Tables 11 and 12 show that the summer of 1947 was very hot, too, as a matter of fact one of the hottest ever experienced in the north of Sweden. In accordance with what has been said above this summer, too, should have had an effect on the whitefish populations. There are, as yet, few analysed scale samples from that year, but material has been collected and in time more light will be thrown on the matter. It may be mentioned here, however, that FABRICIUS (unpublished) has found that the year 1947 is characterized by unusually broad growth zones on the scales of the *aspsik* in Vojmsjön in the Parish of Vilhelmina. That rich year-classes arose that year is apparent from the following data on the *blåsik* in Stora Skeppträsket:

	Born	1948	1947	1946	1945	1944
Catch 1949 (102 specimens)	—	67	18	15	2	—
» 1950 (85 specimens)	—	68	16	1	—	—
Total number of fish caught	—	135	34	16	2	—

Whereas in the late autumn of 1949 the three-summer-old fish were predominant in Stora Skeppträsket, there was, one year later, not one single three-summer-old fish in the samples of spawning fish, the four-summer-old fish being quite predominant, that is the 1947 year-class. The net-meshes used were identical in both years. Apparently a very rich year-class, suppressing the next one, came into being in Stora Skeppträsket in 1947. Year-class 1945, on the other hand, does not seem to have been very rich in this lake, to judge from the figures above, even if unusually many five-summer-old fish may be said to have been contained in the catch of 1949. But in this lake the whitefish die away so quickly that a rich year-class soon disappears altogether, and in the autumn of 1949 the 1945 year-class was five summers old, and thus largely extinct.

Though much more material is certainly necessary in order to analyse more closely the importance of hot summers for survival of fry and individual body growth in whitefish populations, the following three effects of a hot summer may be considered probable:

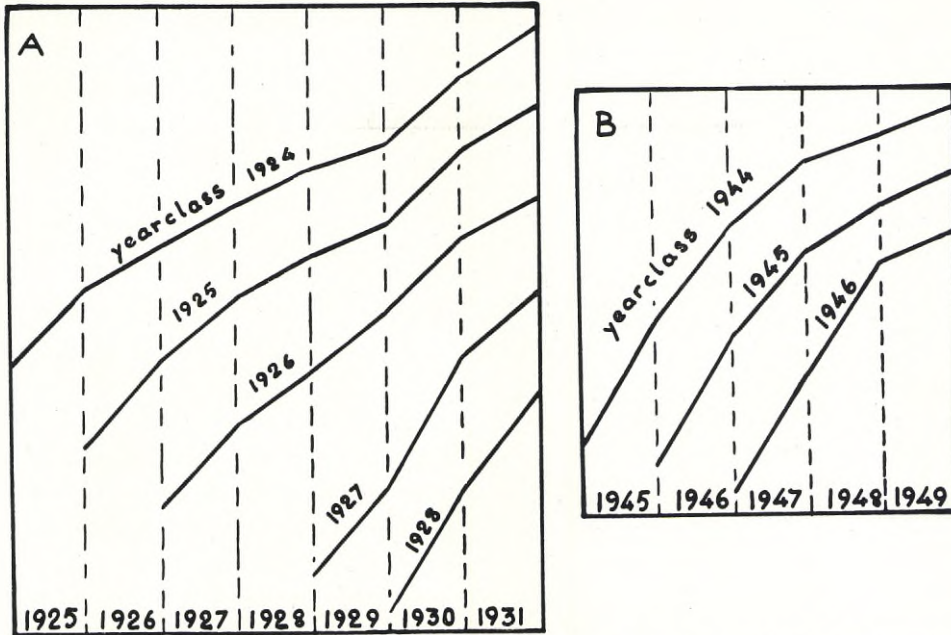


Fig. 3. The response of the whitefish population in Stora Skeppträsket on two hot summers. The growth curves (first summer omitted) of all year classes rose steeply 1930 (A) but not 1947 (B). A strong year class was born in 1947, if this was also the case in 1930 is unknown. The summer of 1930 was hottest in July and August. 1947 was, however, relatively warmest in June.

1. A greater production of plankton and bottom animals than normal.
2. A greater increase in the length and weight of the whitefish during the summer than what is normal.
3. An unusually high survival among the fry that experience their first summer, thus creating a rich year-class.

VAN OOSTEN and HILE (1949) recently pointed out, in the case of Lake Erie, that in this lake the whitefish had a rich year-class in 1926, and they quoted data showing that the fry of six other species in the same lake and in the same year survived very well, and so gave birth to good year-classes. They tried to prove some meteorological factor responsible for this but did not succeed. They do not seem to have studied the summer temperature but only the temperature in spring and a number of other meteorological elements. Perhaps an analysis of the summer temperature would give a better result.

7. Taxonomic Comparison of Three Whitefish Species

Now that we have discussed the samples of *älvsik* in Malå we can make a more systematic examination of the three species of whitefish, the *älvsik*,

Table 13. Growth rate of three whitefish species in different environments; sexes combined. Total length in millimetres.

Species	Lake	Date, sample	1	2	3	4	5	6	7	8	9	10	11	12
<i>Älvsik</i>	Bure River	16.10.1948	121	184	237	287	328	361	382	404	425	446	458	485
<i>Älvsik</i>	Lajnijaur	14.10.1948	111	180	242	292	346	388	409	429	—	—	—	—
<i>Älvsik</i>	Brunträsket	14.10.1948	167	279	341	371	—	—	—	—	—	—	—	—
<i>Storsik</i>	Brunträsket	4.1.1927	139	193	219	237	254	270	276	—	—	—	—	—
<i>Storsik</i>	Brunträsket	{27.12.1949 29.12.1950}	159	248	310	345	363	382	417	440	462	478	—	—
<i>Blåsik</i>	Kälingträsk	15.8.1913	94	179	233	273	300	—	—	—	—	—	—	—
<i>Blåsik</i>	Stora Skeppträsket	15.8.1913	73	106	135	151	159	—	—	—	—	—	—	—
<i>Blåsik</i>	Stora Skeppträsket	23.10.1931	68	101	132	151	159	181	196	203	—	—	—	—
<i>Blåsik</i>	Stora Skeppträsket	27.12.1949	74	121	155	177	190	205	—	—	—	—	—	—

the *storsik*, and the *blåsik*. As has been mentioned before, we use the Swedish names only for the sake of clarity, since the scientific names still are very uncertain.

Of the *älvsik* there are three samples: from their home locality, the River Bure, and from Lajnijaur and Brunträsket. Of the *storsik* there are two samples, from 1927 (only a scale sample) and from 1948—1950, respectively, both from Brunträsket, and of the *blåsik* samples from Stora Skeppträsket 1913, 1931 (only scales) and 1949—50. Moreover, four specimens of *blåsik* from Kälingträsk 1913 are at hand.

a. Growth

Table 13 and Figure 4 show the growth of the whitefish in the various environments.

The *älvsik* displays different growth curves in its three environments. In both the lakes it grows more rapidly than in the Bothnian Sea outside the River Bure. As we know, the samples from Brunträsket only comprised four-summer-old fish, so that this growth curve is very short, but there are some later evidence suggesting that after the fourth summer in Brunträsket there will be a decrease in growth, whereas in the Bothnian Sea the growth will go on for a long time with only a very moderate decrease of the growth increment. It seems probable that the slope of the growth curve depends on the lake, suggesting that a lake can offer good nutrition for young whitefish but considerably poorer amount of food for older and larger whitefish.

The growth rates of the *storsik* in Brunträsket with an interval of 20 years was rather different. From the seventh year the growth figures in Table 13 in 1948—1950 are based only on four fish from the old population (before 1945) and in Figure 4 these values have been omitted. The two growth curves

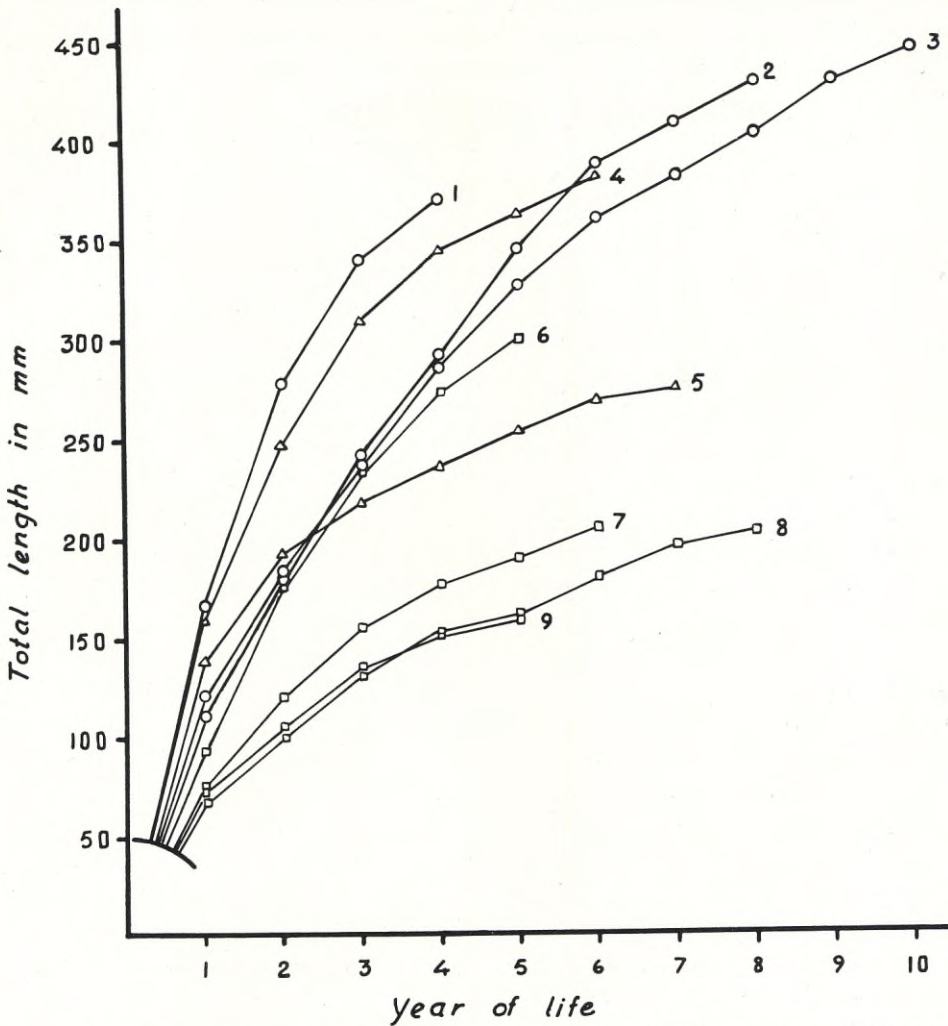


Fig. 4. Growth variation of three whitefish species. *Älsik* (circles): 1. Brunträsket 1948, 2 Lajnijaur 1948, 3 Bure River 1948. — *Storsik* (triangles): 4 Brunträsket 1949—50, 5 Brunträsket 1927. — *Blåsik* (squares): 6 Kålingträsk 1913, 7 Stora Skeppträsket 1949, 8 Stora Skeppträsket 1931, 9 Stora Skeppträsket 1913.

for *storsik* in Brunträsket show similarities in as much as they are strongly levelled out after the first few years' steep rise, which probably indicates a poorer nutritional environment for older fish. Otherwise, they are considerably different and the growth about 1927 was far poorer than when the population was reestablished in 1945. This difference is probably largely due to the numerical strength of the population, *i.e.* the number of fish to share the food. It is not certainly known why the population, which was probably dense about 1927, later on declined so that it almost disappeared.

It is, however, of interest to read OLOFSON's notes from the lake in 1927 saying that the fish »had big heads like whitefish which are dying out». This problem is further discussed on page 116 in this paper.

The *blåsik*, finally, of Stora Skeppträsket is interesting, because it had the same growth in 1913 as in 1931 but later changed to an improved growth in 1949. Nowadays these fish are not heavily fished and the probable responsible change in abundance seems to be spontaneous, like the *storsik*'s in Brunträsket. Moreover these changes have run parallel during the last 20 years and may partly be due to the same factors.

Like other small-sized populations (cf. SVÄRDSON 1949) the *blåsik* of Stora Skeppträsket displayed a striking change of growth when transplanted to a new environment (Figure 1).

Some authors have maintained, that the growth of a certain whitefish species is a hereditary trait. It is admitted that the species which in this paper are called *storsik* and *blåsik* are widespread in Sweden and most often are large and small respectively but nevertheless there are important exceptions to this rule. Fluctuations of growth rate during the decades may be large, however, and when transferred to new environments and thus altered population densities, both species react immediately as demonstrated in Figure 4. The diagnostic value of the growth is restricted to some cases where individuals from two sympatric species are caught at the same time.

Growth, determining spawning size may influence the isolation between species, as further discussed on page 115.

b. Some Morphologic Characters

It has been established before (SVÄRDSON 1950) that, with regard to whitefish, several morphologic characters are dependent on the growth and thus, like it, they are plastic. Moreover, they vary allometrically with changes in the body length. Figure 5 shows the snout-lengths in mm of all the whitefish studied belonging to the three species, in the form of straight regression lines, calculated for each population. The figure shows that the snout is longest in the *ålsik* and shortest in the *storsik*. The earlier transplantations of whitefish from Arjeplog showed that the snout was shortened by an accelerated body growth. This is also in harmony with the fact that when the *ålsik* from Bureå was transferred to Brunträsket, where the growth rate became quicker, its snout became shorter than in the River Bure, its home locality. Thus, it should follow that in Lajnijaur, where the growth was only slightly better than in the River Bure, the snout ought to be longer and correspond to that in the River Bure. As fig. 5 shows, that is not the case at all: the snout in Lajnijaur is even somewhat shorter than in Brunträsket, although the difference is insignificant. The same man measured the fish, so there are not likely to be any errors due to the human factor. On the other

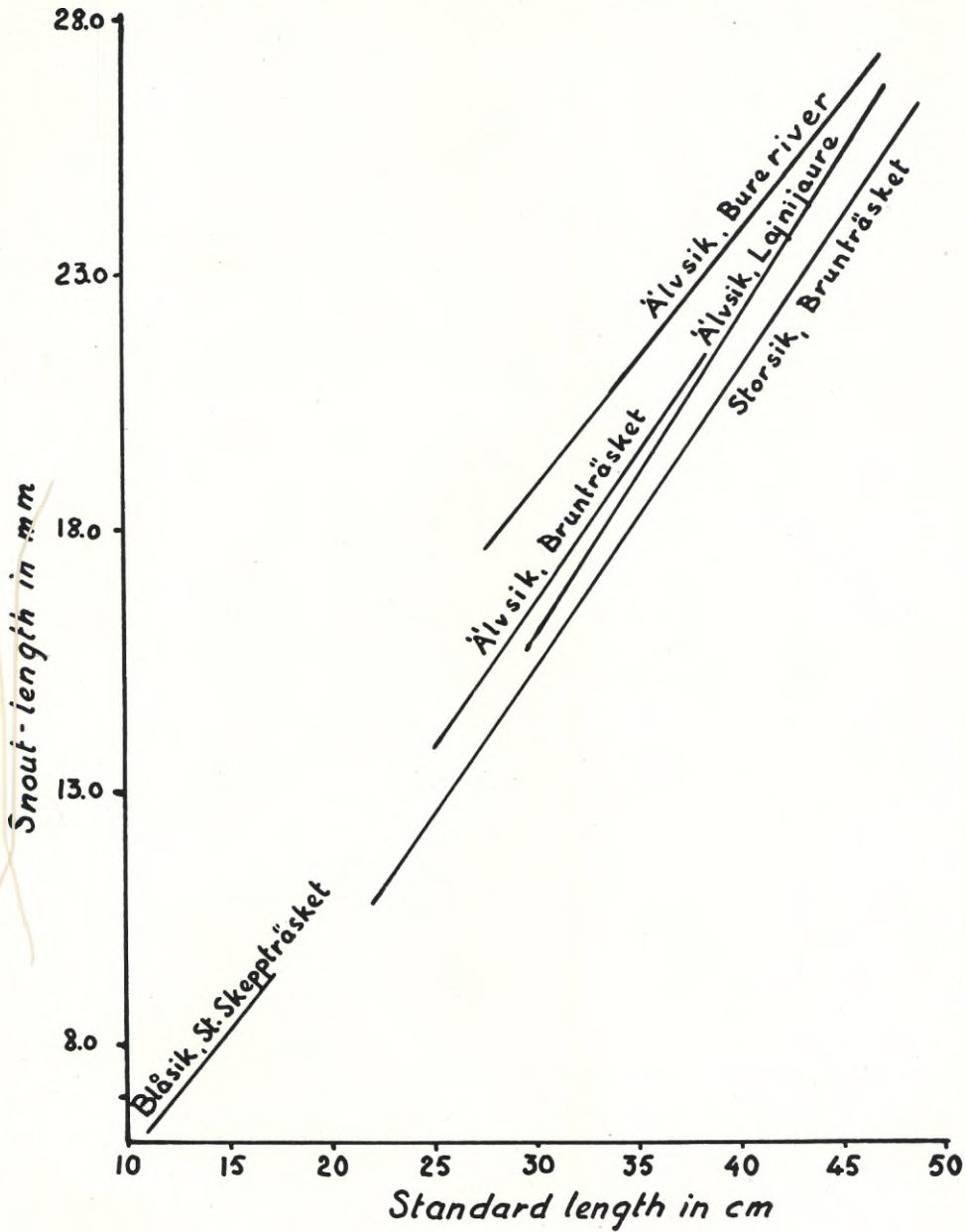


Fig. 5. Length of snout in three whitefish species.

hand, the *älvsik* populations in both Brunträsket and Lajnjaur have grown in fresh water, whereas the *älvsik* in the River Bure grows in the sea outside the river. Therefore, it seems most probable that the salinity also effects the snout-length, inasmuch as a higher salinity tends to give the whitefish

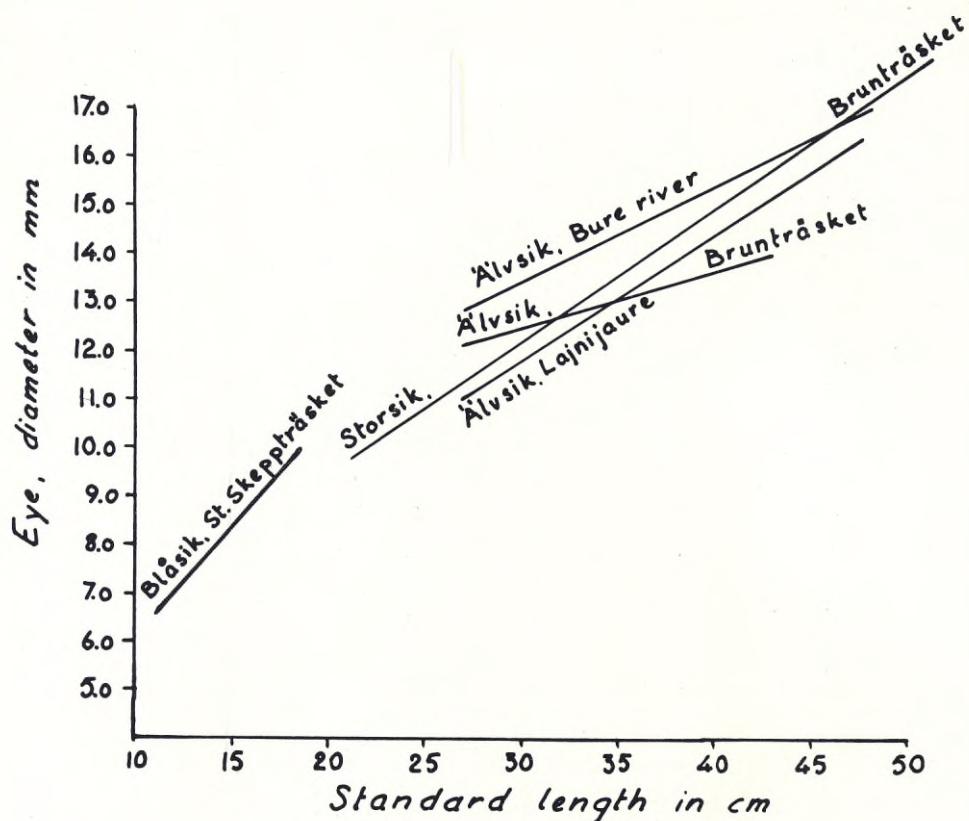


Fig. 6. Size of eye in three whitefish species.

a longer snout. In this connection, it is interesting that the whitefish populations along the east coast of Sweden tend to get longer snouts to the south, so that in the Southern Baltic there occurs a long-snouted »*oxyrhynchus*» species. It is well known that the salinity increases the further south one gets in the Baltic, which may thus be one of the contributing factors.

The *storsik* in Brunträsket has had a poorer growth than the *älvsik* in Brunträsket but better (at least to begin with) than the *älvsik* in Lajnijaur, and so it ought to have a shorter snout than the Lajnijaur whitefish but longer than the *älvsik* in Brunträsket. That is not the case; on the contrary, the *storsik* has the shortest snout of all the populations now studied. This probably implies that the *storsik* has a genetically shorter snout than the *älvsik*.

It is therefore probable that the length of a whitefish snout is dependent on a number of factors, which seem to be the following:

1. The snout-length is closely allied to the body length, so that a larger whitefish has a longer snout than a small one.

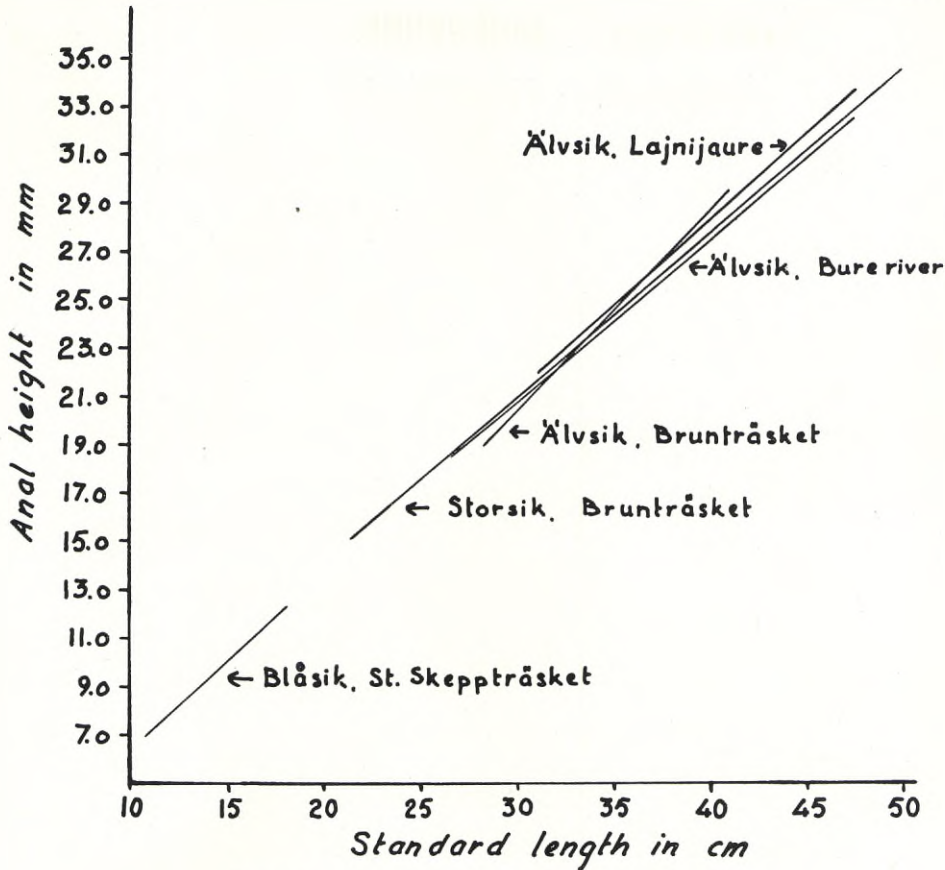


Fig. 7. Anal height in three whitefish species.

2. This relation is modified by the growth rate, so that out of two whitefish similar in size, the one has the shorter snout which has grown most rapidly and thus has the lowest age.
3. The size of the fish and the growth rate being the same, a whitefish living in fresh water has a shorter snout than a whitefish that has grown up in the sea.
4. Besides these three environmental factors (if they may be called so) there is also a genetically varying tendency in different whitefish species, and maybe subspecies, to develop a short or long snout.

In such circumstances it is hardly surprising that in distinguishing different whitefish species the various authors disagree regarding the diagnostic value of the snout-length, and very great caution must be recommended.

As to the size of the eye (Fig. 6), the intraspecific variation is considerable. It has been pointed out before (SVÄRDSON 1950) that a rapid growth changes

the allometry so that the eye becomes proportionally smaller. In accordance with this, the *älvsik* in fresh water has a smaller eye than the *älvsik* of the same size in the River Bure. It is possible that here, too, there may be a modification owing to the salinity of the water, but the material is not so convincing as was the case of the snout-length, particularly as the regression line for the relation eye/body length of the *älvsik* in Brunträsket has quite another inclination than the other lines, which probably is an artifact. The *blåsik* in Stora Skeppträsket has a comparatively large eye, which is typical of young whitefish or such as show juvenile characters.

The height of the tail, in front of the caudal fin, is shown in fig. 7. No differences in this character seem to exist between the populations studied.

c. Scales

The number of scales in the lateral line have been studied in all the populations, and the results are accounted for in Table 14. There is a difference between the three species, since the *älvsik* have an average of 97—98 scales, the *storsik* 94, and the small *blåsik* as few scales as 81—84. When whitefish from Uddjaur (SvÄRDSON 1950; see also Map 1) were transferred to Kälarne, it was pointed out that the difference between two whitefish species in Uddjaur — which was, on the average, 3 scales — was a pure temperature modification due to the date of hatching, for when the two species grew up in small ponds with the same temperature the two species got the same number of scales, in both cases fewer than in their home lake. As the *älvsik*, too, spawns in October, at about the same time as the *aspsik* in Uddjaur, whereas the *storsik* in both cases (both Uddjaur and Malå) spawns at Christmas — New Year, the difference between *älvsik* and *storsik* in the Parish of Malå is probably a pure temperature modification, too, owing to the fact that the *storsik* is hatched later and its number of scales is determined later when it lives in warmer water. It is remarkable that the *storsik* in Uddjaur and the *storsik* in Malå, which, judging from many signs, are populations of one and the same whitefish species (with a wide distribution all over the north of Sweden), have practically the same number of scales in their home waters. We must, of course, not overlook the fact that in the case of output of fry, a measure which of course, is common in all experiments and transfers of whitefish from one environment to another, these fry may be put into the lake at a time which is »biologically wrong» for the species in question, and so they may react, for instance, with a number of scales that is considerably different from what is otherwise normal. The case will be another if the whitefish themselves may spawn in the lake, if the spawn may develop slowly during the whole winter and the fry be hatched in due time. It is very possible that the morphological characters sensitive to temperature, such as number of scales, vertebrae, fin-rays, etc.,

Table 14. Number of scales in the lateral line of three whitefish species.

Species and locality	73	74	75	76	77	78	79	80	81	82	83	84	85	86
<i>Älvsik</i> , Bure River	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Älvsik</i> , Brunträsket	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Älvsik</i> , Lajnijaur	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Storsik</i> , Brunträsket	—	—	—	—	—	—	—	—	—	—	—	—	1	—
<i>Blåsik</i> , St. Skeppträsket, 1913	—	—	—	2	1	1	2	2	2	3	—	—	2	2
<i>Blåsik</i> , St. Skeppträsket, year-class 1947	1	—	—	—	—	2	4	5	7	14	16	13	10	13
<i>Blåsik</i> , St. Skeppträsket, year-classes 1944—46	—	—	—	—	3	—	3	2	5	4	4	7	5	3

Species and locality	87	88	89	90	91	92	93	94	95	96	97	98	99	100
<i>Älvsik</i> , Bure River	1	—	1	1	5	4	3	8	13	6	8	8	7	5
<i>Älvsik</i> , Brunträsket	—	—	—	—	—	3	3	2	4	7	5	7	5	5
<i>Älvsik</i> , Lajnijaur	—	—	1	—	3	1	—	3	2	2	4	2	—	1
<i>Storsik</i> , Brunträsket	—	—	2	2	4	5	5	3	4	4	5	3	1	—
<i>Blåsik</i> , St. Skeppträsket, 1913	—	—	1	—	—	—	—	—	—	—	—	—	—	—
<i>Blåsik</i> , St. Skeppträsket, year-class 1947	14	6	4	5	—	—	—	—	—	—	—	—	—	—
<i>Blåsik</i> , St. Skeppträsket, year-classes 1944—46	4	4	1	—	2	—	1	1	—	—	—	—	—	—

Species and locality	101	102	103	104	105	106	107	108	109	Number of specimens	Average
<i>Älvsik</i> , Bure River	10	5	4	4	2	—	2	1	—	98	97.59
<i>Älvsik</i> , Brunträsket	5	1	—	—	—	1	—	1	1	50	97.82
<i>Älvsik</i> , Lajnijaur	5	1	3	1	1	1	—	1	—	32	98.16
<i>Storsik</i> , Brunträsket	1	1	—	—	—	—	—	—	—	45	94.12
<i>Blåsik</i> , St. Skeppträsket, 1913	—	—	—	—	—	—	—	—	—	18	81.33
<i>Blåsik</i> , St. Skeppträsket, year-class 1947	—	—	—	—	—	—	—	—	—	114	84.21
<i>Blåsik</i> , St. Skeppträsket, year-classes 1944—46	—	—	—	—	—	—	—	—	—	49	84.12

will then display a much smaller variation than in the case of transfers, since the fry even during their embryonic stage in winter, by an accelerated or retarded growth rate are able to adapt themselves to the normal temperature curve of the water and consequently pass through the stages affecting the various characters in approximately the same temperature environment. An example of this is probably afforded by the *blåsik* in Stora Skeppträsket, and the 1947 year-class from that lake has been dealt with separately in Table 14. As the warming-up of the water started early in that hot summer

(even during the spring months) this year-class should — theoretically at least — perhaps display a smaller number of scales in the lateral line, on account of the warmer water. As Table 14 shows there is, however, no such difference between the year-classes, and this is probably due to the fact that the whole development is accelerated at the warming-up of the water, so that in a hot spring the stage critical for the formation of scales in the lateral line is passed earlier than normal, but in water of about normal temperature.

In 1913 the *blåsik* population of Stora Skäppträsket had only 81.33 scales in the lateral line but in 1949—1950 the average was 84.18. The 1913 sample is small and comprises only 18 fish but nevertheless the difference between the averages is statistically significant. The probability (P) that chance alone was responsible for the difference lies between 0.01 and 0.001. Since temperature in this case seems to be excluded as the causal factor, something else must be sought for. The size of the eggs probably is this second factor. From Table 13 it is evident that the *blåsik* in 1913 were smaller than in 1949. TOORS (1951) has found the eggsize of whitefish to be positively correlated with body length. Thus in 1913 the spawned *blåsik* eggs probably were somewhat smaller than those spawned in the late forties and consequently the fry must have had a proportionate difference in size. To the best of my knowledge there is no experimental evidence suggesting that a smaller fry, other things being equal, gets a lower number of scales. As, however, all small-sized whitefish populations, studied so far by the present writer, have had fewer scales than the large-sized populations, a positive correlation seems rather probable. Unfortunately no exact data on the diameter of the eggs are at hand. But the circumstantial evidence suggests that the number of scales is due to the size of the fry, that is, the size of the eggs and, finally, the body length of the parent fish.

Thus we are faced with the possibility that the large difference in scale-number between the *storsik* and the *blåsik* of the Malå lakes (more than ten scales on the average) may be due to the different sizes of the parent fish. As growth is plastic and highly modified by the environment we must judge the number of lateral scales as also very strongly modificational.

d. Gillrakers

The number of gillrakers on the first left gill-arch have been counted on all the whitefish studied and the result will be found in Table 15. There the various samples have been grouped according to year, so that the variation may be better illustrated.

The table shows that the *storsik* in Brunträsket has the smallest number of gillrakers, an average of about 24, and with a total known variation of

Table 15. Number of gillrakers on the first left arch in three whitefish species.

Species and locality	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	Number of specimens	Average
<i>Älvsik</i> , Bure River																												
16.10.1948	—	—	—	—	—	1	6	15	11	17	16	13	12	6	1	—	—	—	—	—	—	—	—	—	—	—	98	28.45
<i>Älvsik</i> , Lajnijaur																												
14.10.1948	—	—	—	—	1	—	2	1	2	4	5	5	3	5	1	3	—	—	—	—	—	—	—	—	—	—	32	29.63
<i>Älvsik</i> , Brunträsket																												
14.10.1948	—	—	—	—	—	1	1	2	4	11	4	8	9	3	7	—	—	—	—	—	—	—	—	—	—	—	50	29.58
<i>Älvsik</i>	—	—	—	—	1	2	9	18	17	32	25	26	24	14	9	3	—	—	—	—	—	—	—	—	—	—	180	28.97
<i>Storsik</i> , Brunträsket																												
14.10.1948	1	—	—	2	2	1	2	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	23.70
27.12.1949	—	1	1	5	3	1	4	1	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	19	23.74
29.12.1950	—	1	2	2	—	3	3	3	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	24.13
<i>Storsik</i>	1	2	3	9	5	5	9	5	4	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	45	23.87
<i>Blåsik</i> , St. Skeppträsket																												
13.8.1913	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	4	5	6	5	3	2	2	31	39.96
27.12.1949	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	8	17	25	16	10	9	4	—	93	39.35
29.12.1950	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	7	9	21	19	12	9	3	2	85	39.71
<i>Blåsik</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	7	18	30	51	41	27	21	9	4	209	39.59

19—28. The three samples show, as is apparent, quite similar figures, and the difference between the average values is statistically insignificant.

The *blåsik*, the other whitefish species native in Malå, has a considerably higher number of gillrakers with an average of 39.6 and a total known variation of 35—44. Here, too, the three samples agree completely. It is interesting that during a period of 37 years no change has occurred.

The third species introduced into Malå, the *ålsik*, is intermediate as to the number of gillrakers with an average of 28 or 29 and a total known variation of 23—34. Thus, the three species are well separated in their averages, although the variation is so great that overlapping occurs between *storsik* and *ålsik*. It is of particular interest to see how constant was the number of gillrakers of the fish transferred from the Baltic to the lakes in Malå. In the Baltic the average was 28.45, in Malå 29.63 and 29.58, respectively. Thus, the number of gillrakers increased by about one unit as a consequence of the transplantation, and the difference between the River Bure and the Malå lakes is statistically significant. Consequently, the number of gillrakers changed owing to the transplantation, but the change was small.

It may be thought that this change was caused by selection in that such whitefish fry as had a small number of gillrakers were not able to compete but were eliminated and the number of survivors got a higher average than the fry had as newly hatched. In order to test this hypothesis, the growth of the *ålsik* in Brunträsket was studied, both of those which had fewer gillrakers than 29, and of those which had more gillrakers than 29. The two groups comprise 19 and 27 specimens, respectively, and their reconstructed length at the end of the first year (before possible sexual differences have appeared!) was 168 and 167 millimetres, respectively. In other words, they were the same size. In such circumstances, fewer survivors in the group with a small number of gillrakers does not seem at all probable, not even at the fry stage. For a handicap in the taking of food, so serious that it leads to death, should, of course, also — and more easily — be noticed as a handicap in the power of growth, which can hardly have been entirely compensated later on during the rest of the first summer. A selection, eliminating animals with a small number of gillrakers, is thus not probable.

That leaves us only the possibility that the number of gillrakers was modified by environmental factors of some kind. It seems probable that the most important of these is the salinity, even if the temperature may have played a part, too. The conception that the temperature is an active factor is, however, contradicted by the circumstance that the *ålsik* have approximately the same number of scales in the lateral line in the River Bure as in fresh water in Malå. Moreover, the number of gillrakers is determined quite late (cf SVÄRDSON 1950), which also contradicts the idea that during a certain »critical period» the temperature is an influencing power. As was true of the

snout-length, the most probable factor seems to be one connected with the character of the water.

Thus, even if it has been proved that the number of gillrakers may be modified by environmental factors, this modification is nevertheless insignificant compared to the obviously genetical constancy shown by the gillrakers and which is, in some ways, in contrast to most other taxonomic characters in whitefish. As was true of the transplantation of the Uddjaur whitefish, the transfer of the *älvsik* from the River Bure has emphasized the value of the gillrakers as a taxonomic aid.

8. The Mechanism isolating Different Coregonid Species

In his description of Lake Vättern TISELIUS (1723) treated, among other things, its fish and writes that there were three species of whitefish in the lake, besides the small whitefish (*Coregonus albula*), and gives them the names *asp*, *stensik* and *gråsik*. These names are still used round the lake to describe different species of whitefish. TISELIUS writes about the *asp* that it has only few spawning places which he names, among others a point at Kråk, and at this place the whitefish still spawns. Moreover, at Aspa in the northern part of the lake, the species called *asp* still spawns and from this locality it certainly has got its name though this was not mentioned by Tiselius (cf. Ekman 1916). So there can be no doubt that the whitefish of Vättern have remained isolated from each other as distinct species for at least about 250 years and probably much longer. The spawning places seem to have remained unchanged, too.

In a similar manner SILJESTRÖM (1730) described the large lake Siljan in Dalarna, and he, too, deals with the fish of the lake, and among them, of course, the whitefish. Besides *Coregonus albula*, SILJESTRÖM also knows three species of whitefish in Siljan, viz. *ryssing*, *djupsik*, and *grönsik*. These names are still used, though the last species nowadays also is called *grundsik*, a name which sounds very similar to *grönsik* (LUNDBERG and WAELBERG 1892, ARWIDSSON 1913). The *ryssing* is said to be a small-sized whitefish; there is a picture of it, too; it spawns in some named brooks running down to Siljan. To this day the *ryssing* spawns in these brooks and it is still fairly small. The spawning time does not seem to have changed, either.

In his notes from Sundsjön in Jämtland published by HASSELBERG (1930), FALE BURMAN mentioned *storsik* and *småling* in 1790 and these species are still living in Sundsjön, well separated from each other as to habits and gillrakers, and still being called by the same local names by the people.

It is evident from these examples that the whitefish have been well known in Swedish lakes for several hundred years, that they still have their local names, that the spawning periods are the same, and that, in several cases, the same restricted spawning places have been used for at least two hundred

years. Thus, the question of the isolation of the species, which seems to be very efficient in nature, is a question of what factors affect and regulate the spawning.

In the river Bure the *älsik* normally spawns about 10—25 October, and when these whitefish were transferred to the lakes in Malå it turned out that it spawned at about the same time there. According to supplementing studies carried out by PETERSON in 1949 and 1950 the spawning time would seem to be, on the average, a few days earlier in Lajnijaur, at least. In Brunträsket it is more difficult to date the spawning period, since fishing during spawning time has been prohibited there to improve future fishing. When, in October 1948, the temperature was measured at all three places, it was found that it was about the same, approx. 2.8° Centigrade, but this may have been a coincidence. In Malå the water is probably cooled down somewhat quicker owing to its geographical situation. The spawning bottom used by the *älsik* was the same in all three places, that is bottom with big stones. Also the depth was the same.

When the Uddjaur whitefish were transplanted to the neighbourhood of Kälarne (SVÄRDSON 1950) it seemed as if the two species transplanted on the whole retained their different spawning periods, although it was not possible to obtain full proof of it.

With regard to the whitefish in Vojmsjön, FABRICIUS (1950) has been able to prove, and that convincingly, that the spawning period of one and the same whitefish species may be very protracted and at the same time that it chiefly seems to be determined by the demands of the fish for a particular type of spawning ground, and by the temperature conditions over that very ground. Thus, the three species of whitefish in Vojmsjön have, at some places, different spawning periods whereas at others they spawn at the same time, although on different bottoms and consequently different depths. Particularly the *storsik* in Vojmsjön, which spawn at the smallest depth and on a firm bottom, showed a very marked difference in the spawning time at different strips of shore along the large lake. FABRICIUS points out, too, that, although the differences in spawning times may be genetically fixed, such genetical differences must be very difficult to prove, owing to the demonstrated influence of the bottom and the temperature of the water.

With regard to mammals and birds modern ecological studies have shown that the breeding occurs so that the young are in their greatest »food-requiring» period at the time when suitable food is most easily available in nature. These warm-blooded animals have a mechanism which, with the aid of the varying length of day-light, regulates their sexual functions. In fish, too, it has, in some cases, been possible to prove (for literature see HARRINGTON 1950) that the varying period of day-light has an influence on their spawning activities. From an evolutionary point of view it may be maintained that if the date of the spawning period is determined by the

number of surviving fry many months later (ultimate factor), it should be very »risky» to let the time of spawning be decided exclusively by so variable a factor as the water temperature (proximate factor). The season should be important as an extra »corollary». Therefore it seems probable that the experiments which have already been made and which show that the amount of light plays a certain part in determining the spawning of fish, are of rather general applicability.

Thus, even if, in the case of the whitefish, the amount of light, and so the »season» may play a part in determining the spawning time, we have not obtained any proof that different species of whitefish differ in this character. I share FABRICIUS' (*op.cit.*) view that no evidence have as yet been brought forward of genetical differences in the spawning times of different whitefish species, and the fact that the *storsik* in Vojmsjön and neighbouring lakes can spawn for a period of five months shows that quality of the bottom and the temperature of the water may cause all the differences so far known between different species of whitefish.

Differences of spawning periods and depths certainly are important for the isolation of sympatric whitefish species. Ethological differences in spawning behaviour may exist, but nothing is known at present about this topic. The smell of whitefish, which can be easily recognised by a human being, may have a biological function, stimulating schooling and there may be differences in this smell which we cannot feel. »Imprinting» may further cause the return to restricted spawning localities, but nothing is certainly known about it at present.

It is very striking that sympatric whitefish species most often have different spawning sizes, *i.a.* different growth rates. Earlier in this paper it has been stated that differences in growth rates cannot be looked upon as genetical properties of the different species. But there remains the possibility that growth has a fundamental consequence for the isolation of species. In Lake Storsjön in the province of Härjedalen there are two whitefish species, *storsik* and *blåsik* with different mean sizes and very different number of gillrakers. In a sample of spawning *storsik* two specimens of *blåsik* were found (which was evident on the gillrakers) but these two fish were 10 centimetres larger than the average spawning *blåsik* population. They were schooling with the *storsik*, which had the same larger size. In the sample of spawning *ålsik* from Lake Brunträsket, mentioned earlier in this paper, the participating *storsik* were of the same size. On the other hand FABRICIUS (unpublished) have found that two sympatric species in Lake Dikasjön are of very different size and moreover, that one of the species often move over the spawning grounds of the other but no hybrids are formed, as judged from the number of gillrakers in the populations, though spawning periods coincide. There is some further evidence that size may contribute to the isolation between sympatric species, especially where their spawning periods overlap.

The occurrence of hybrids in nature is very difficult to elucidate. This is mainly due to the fact that the cryptic species are so difficult to identify themselves, as most of their morphological properties overlap. Russian authors have claimed that the species sometimes do hybridize, but the evidence is meagre. WIESE (1942) reported some facts from East Prussia which indicate the occurrence of hybrids. JÄRVI (1940) closely studied the introduction of two different species of whitefish in Lake Pyhäjärvi and the gillrakers (Table 16) indicate that these two species have produced hybrids in the lake. JÄRVI does not mention this in his report but he states that growth is similar in both species. So far the Pyhäjärvi-case seems to be the best evidence of hybrids in whitefish.

It is completely unknown so far, if the vitality or fertility of the hybrids are the same as that of the pure species. JÄRVI found, however, that growth of the two species (and their hybrids) in Pyhäjärvi was improved during a long period, which probably means that the number of fish decreased. Such a spontaneous reduction of the population might have been due to lesser fertility of the hybrids. In Lake Brunträsket, OLOFSSON found 1927, as cited earlier, that probably two »forms» of whitefish were living and also that they looked as »dying out». Later the whitefish population of Brunträsket had a crash and before the *älvsik* was introduced in 1945, only *storsik* was left in stray specimens while the *blåsik* had disappeared. As a hypothesis, therefore, the crash might be said to have followed the production of hybrids in too great scale. There are other cases known where a whitefish population (or two different species being of roughly the same size) has crashed in few years, without intensive fishing.

From the distribution of the different whitefish species in both Finland and Sweden it can be inferred that one species probably has ousted another from large areas. This can have occurred as competition for food but also by swamping, one species partly participating in the spawning of the other.

STEINMANN (1950) in his monograph on the Swiss whitefish populations could not agree to the conception advanced here of the whitefish as a group of closely related cryptic species. He develops ideas, according to which the recent whitefish populations should be subspecies, arisen through evolution, by means of ecological isolation, within the different lakes. Consequently, parallel types in different lakes are looked upon not as derived from one parental population but instead as radiation adaptations, repeated in almost every lake, from a common ancestor, »Urfelchen» or »*Coregonus primigenius*». STEINMANN'S »new system» in whitefish taxonomy breaks down completely when confronted with Swedish whitefish populations. The probability that a »*Coregonus primigenius*» should have in every lake splitted into the *storsik* and the *blåsik* of certainly a thousand swedish northern lakes seems very small indeed, especially when this process simultaneously should

not have taken place in most of the Finnish and South Swedish lakes (cf. JÄRVI 1943)! Moreover, this evolution should have occurred during some few thousand years and by means of ecological isolation instead of geographical (cf. BROOKS 1950). Finally, the term »ecotyp» or »subspecies» does not at all suite whitefish populations, living in the same lake for hundreds of years with no hybrids at all or, sporadically, some stray such specimens. There seems to be no other taxonomic term for such populations than »species», irrespective of the possibility that they in some cases swamp each other by mass hybrids, when the isolating barrier has been broken down. Nor can it seriously be doubted that they have invaded Scandinavia as separate populations, already different in the number of gillrakers etc.

9. Nutrition and Changes in Physiological Aging

The *blåsik* in Stora Skeppträsket is an example of a whitefish population which is distinguished by a poor growth, early sexual maturity, short span of life, and persistency of a number of juvenile characters as to morphology. Such whitefish populations are common, and the problem they offer is the same as that offered by populations of small-sized trout, char, brook trout, and salmon, and by »kokanee» in British Columbia (cf. FOERSTER 1947, RICKER 1950). In some respects they constitute a sexually mature stage of young animals and they seem to remain at a stage of development which whitefish of other populations pass early in their individual lives. The most essential fact seems to be that the aging itself is different. A short survey of a few recent data on aging may therefore be justified.

In an interesting study on obesity in children MOSSBERG (1948) has proved that variations in aging may arise even during infancy. Fat children are fat because they eat more than other children, and we may disregard the question whether this is genetically determined or not. The richer supply of calories has some characteristic results for these children as compared to normal children. They seem to have a higher total basal metabolism, and during the course of their development they show a number of characteristic features, which may best be summarized so that they are before normal children in their development, thus older than them, counted in physiological age. They are taller, they experience the accelerated increase in length before the puberty earlier than other children, pass through puberty earlier, display skeletal features indicating a higher age and, finally, their intelligence develops more rapidly. It is very interesting that, in spite of their being earlier than other children in their development, they are, as adults, somewhat shorter than the average.

For several years BONNIER and his collaborators have experimented with breeding identical twins of cattle on different nutrition standards. They have

then found that the nutrition affects aging, so that animals with a rich supply of food age more quickly. The sperm production of bulls begins later in animals which have obtained less food, the change of teeth occurs later, too, and in a case when two twin heifers were reared for four years on different nutrition standards, the one that got most food was before the other in development the whole time. Both of them had a genetical disease, a hormonal disturbance causing them to become nymphomatic, and this change occurred at the age of 2 in one of them, but in the other at the age of 3.5 (HANSSON and BONNIER 1950). The fact that a genetical disease comes earlier when there is a rich supply of food is of great interest, since in the case of human beings, it has been proved that a genetical disease sometimes shows a tendency to arrive earlier with every new generation (GATES 1946). This phenomenon has been called »anticipation». During the last few generations the standard of living has been raised, so that the explanation of this phenomenon may very well be an increased supply of nutrition and with that a more rapid physiological aging.

GUNTER (1950) has proved differences to exist in the size of several species of fish along the east coast of America and has established a relationship between these differences and the temperature of the water. At the same time he gave a review of the quite extensive literature on the subject, which shows that animals in warm seas differ from those in cold seas by having a more rapid growth, an earlier sexual maturity and an earlier death, a smaller number of scales, vertebrae and fin-rays, and other meristic characters and a smaller body size. »Delayed sexual maturity, longer life, slower growth and greater final size are characteristics of animals in colder seas» (GUNTER, *op.cit.*, p. 299). He warns, too, against considering such differences to be genetically fixed. Even if, in this case, the lower temperature lowers the metabolism and this low metabolism is the active factor in the delayed aging in cold water, a rich supply of food seems, on the other hand, to increase the metabolism (MOSSBERG, *op.cit.*) so that there will be a certain parallelism between the effect of a low temperature and a low nutritional standard.

Thus, it is very tempting to look for a general explanation of all these phenomena, that is slow aging when the metabolism is low and quick aging when it is high.

In the case of a whitefish, for instance, the head is comparatively big in a very young fish and its size then diminishes, relatively, as the whitefish grows bigger and older. A big head is thus a »juvenile» character, and when it turns out that, when whitefish are transplanted (SVÄRDSON 1950) the head becomes relatively smaller in whitefish with a rapid growth (and a rich supply of food), this implies that the whitefish have »aged» more rapidly as a consequence of a rich supply of food. The same applies to the size of

the eye, and a number of other body proportions. That the relation between the whole body and one single organ now and then changes by leaps (MARTIN 1949) does not effect this phenomenon.

In *Lebistes* (SVÄRDSON 1943) a rich food supply causes an early sexual maturity and so a fairly long final body size. The physiological aging has been accelerated as compared to the calendric age. If the food supply is somewhat lower the growth becomes slower, the aging, too, and so the final size will be greater than in the first case. But when the nutritional standard is really low there appear »hunger-forms» which, to begin with, grow very slowly but nevertheless reach a fairly early sexual maturity, and their final size is smaller than that of the other animals. That sexual maturity is accelerated when the nutritional standard is really low seems to be typical of fish and possibly of other cold-blooded vertebrates living in water. If there is a fish population in a lake where the amount of food per individual fish constantly sinks, for instance because of a continuous increase in the population, this change implies a retardation of the growth and an increased tendency to »slow» aging. If the sexual maturity followed the general retardation, it would be more and more delayed and, finally, the fish would not attain it at all. It seems near at hand to suppose that under such conditions the natural selection will favour such animals as possess a hormonal mechanism permitting sexual maturity to appear early as compared to other physiological functions. Thus, there must be a selectional pressure with the effect that sexual maturity is quickened if the nutrition standard becomes too poor. In the case of *Lebistes* it is interesting that the size of the testicles follows that of the body but that the spermiogenesis itself appears in a younger and smaller testicle when the supply of food is poor.

We may arrive at a plausible explanation if we suppose that the spermiogenesis and oogenesis, which, as is well known, are differentiation processes, are favoured by a poor supply of food in contrast to other differentiation processes but that at the same time they are dependent on a certain gonad size to be able to begin. Therefore, sexual maturity will be delayed as long as the gonad is delayed but yet it will be comparatively earlier when the supply of food is poor than when it is moderate.

Thus, sexual maturity is probably modified to a fairly large extent according to the food supply. And then there is the possibility of such populations arising as are called »sexual mature juvenile forms». They should arise when the food supply is extremely poor, perhaps also as a result of extremely low temperatures. Besides, it seems as if physiological death follows sexual maturity in so far as an individual or a population that attains an early sexual maturity also dies earlier. This is very striking in the different sexes of many fish, the males, as a rule, being sexually mature one or two years earlier than the females and also dying earlier. A rich year-class of trout

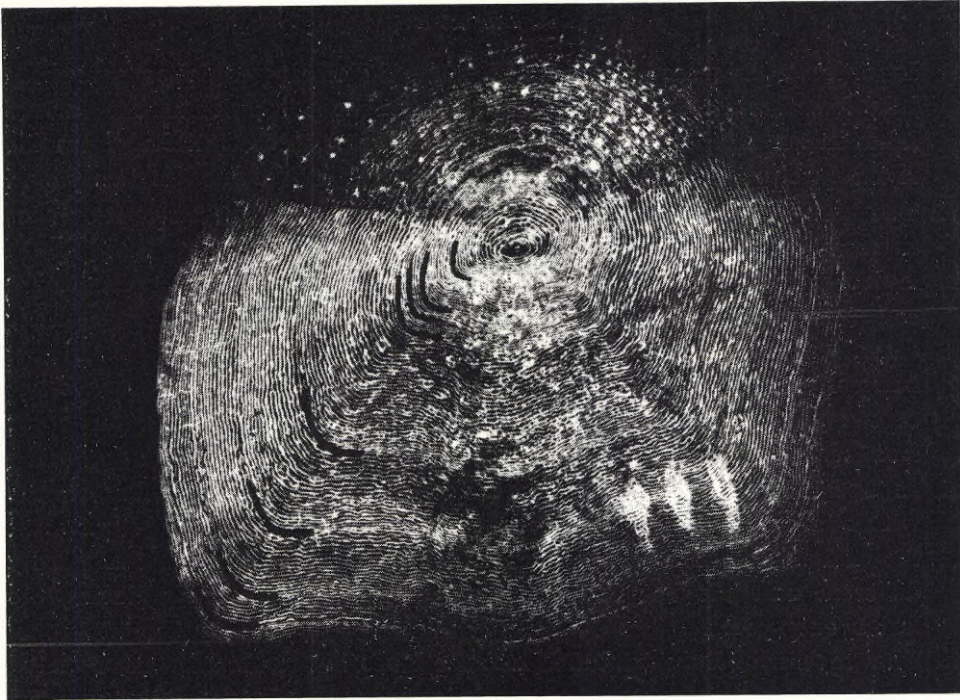


Fig. 8. Scale of a four-year-old spawning whitefish of the dwarfed population in Lake Rissjön retaken five years after its transfer to Lake Vänjaurträsk. Total length had improved from 16 cm to 39 cm and the weight 20-fold. The span of life was considerably increased by the experiment. The phenomenon has been well-known for centuries in northern Sweden and has been utilized in a great many small lakes with no spontaneous fish population.

or salmon, for instance, which may be followed by the fishermen for many years, finally consists of chiefly females (cf ALM 1950). The same applies to *Coregonus albula*, pike and perch, and many other species.

Dwarfed populations, such as that of *blåsik* in Stora Skepträsket have slow growth, early maturity and a short life-span. The length of life, however, may be altered by experiment. The famous small-sized whitefish of Lake Lomsjö (cf OLOFSSON 1934) was transferred in the late twenties to a couple of lakes, among them Rissjön. Here it first grew better than in Lomsjö, later, however, worse. From Rissjön it has in the forties been transplanted, as spawning adults, to new lakes again. Then growth improved as usual. The present Rissjö population has an average individual weight, when spawning, of 36 grammes (ÖQUIST *in litt.*) and an age of 4–6 years. The transplanted fish have reached a weight of 700–1,000 grammes in Lake Vänjaurträsk. Their scales (Figure 8) show the improved growth and the increased length of life. Probably their life-span can be almost doubled by transfers to better nutritional conditions.

10. Summary

1. In order to increase the yields of whitefish fishing in lakes, numerous transfers of whitefish have been made from the Northern Baltic to various lakes in the north of Sweden. The transplantation of whitefish from the river Bure to the lakes in the Parish of Malå is discussed in this paper.
2. The Bure whitefish spawns in the river but grows up in the sea. It spawns in the middle of October and the fishing of it is described. The growth is poorer than in the case of the same species of whitefish further to the south on the coast. The males do not grow so fast as the females after sexual maturity has been attained. No differences in the growth exist between whitefish with the same number of gillrakers as the average of the population (27—29) and such individuals as have a larger or smaller number.
3. In the Parish of Malå there are two sympatric species of whitefish, *storsik* with about 24 gillrakers and *blåsik* with about 39. They both spawn at the end of December but on different bottoms. The growth is markedly different and has, for both of them, changed considerably during the last twenty years.
4. The transfer of Bure whitefish into the lakes in the Malå Parish resulted in large populations and enormous yields of whitefish in Lajnijaur and Brunträsket. They were identified as Bure whitefish by their number of gillrakers, their choice of spawning bottom and spawning time (October). A sample of the Bure whitefish was found to contain, too, some specimens of *storsik*. It is often difficult to distinguish different species of whitefish obtained together in the gill nets but it is very important for the determination of the variation of the taxonomic characters. In this case a method was used in which several different characters were considered at the same time.
5. A hot summer may cause a better growth than what is normal in the whitefish in the north of Sweden and may give birth to a rich year-class. The effect of the hot summers of 1930, 1945, and 1947 on the whitefish populations in Malå is discussed.
6. An examination of the value of some taxonomic characters disclosed that:
 - The growth is plastic and dependent on the amount of food available for each individual and the general nutritional and temperature standard of the lake,
 - the snout-length varies with the body length, with the growth rate, with the salinity of the water and probably, too, with genetical differences between different populations,
 - the relative size of the eye decreases when the growth is rapid,
 - the number of scales in the lateral line varies with the temperature of the water, and consequently with the spawning time and the ecological

habits of the population, and probably it is correlated with the egg-size and thus dependent on the growth of the parent fish.

the number of gillrakers is affected by the body size (under a certain limit, cf SVÄRDSON 1950) and to some extent probably by the quality of the water, but it is chiefly genetically based.

7. The isolation mechanism between different whitefish species is discussed. Different spawning periods arise when the whitefish prefer different bottoms and different depths where the optimal temperature is reached on various dates. The »season» possibly may also influence the spawning of different species. Size may sort out schooling individuals and so contribute to the isolation. The coexistence of sympatric species in some lakes for two centuries is known. Hybrids seldom occur but they might be involved in the crash of some populations and when one species oust another. It is argued that sympatric populations must be ranked species and not »subspecies» or »ecotypes», and further that they have not developed within their present home-lakes but invaded them after the glaciation.
8. The connection between food supply and physiological aging is discussed. There is evidence that a rich food supply accelerates the physiological aging and *vice versa*.

Exceptions are the spermiogenesis and the oogenesis, which seem to be accelerated when the food supply is poor. This is interpreted as the result of a selection as sexual maturity cannot, without serious disadvantages, be delayed like many other differentiation processes. An early sexual maturity and a short span of life is typical of whole populations and might be modified in experiment. In many species of fish the same relation exists between the sexes in that the males, who attain an earlier sexual maturity than the females, also die earlier.

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An Investigation of Some Factors Affecting the Upstream Migration of the Eel

By INGEMAR SÖRENSEN

It has been established at elver-catching stations in different waters that elvers do not migrate upstream until the water temperature exceeds a certain threshold value. At the catching station at Trollhättan no appreciable numbers of elvers made their way upstream until the water temperature had reached 15° C. or more during the period 1919—1950. A slightly higher temperature limit was recorded at the elver-catching station built by the paper mill, Aktiebolaget Klippans Finpappersbruk, in the River Rönneån. Other factors, such as light and current conditions, also affect the upstream movement of the eel. The literature, however, contains but few experimental investigations of the significance of these factors, and that prompted the experiments described below. The main object of the studies was to investigate the capacity of eels measuring 7 to 30 cm to make their way upstream against strong currents. In the experiments the role played by water temperature was taken into account, as it was thought probable that this factor affected the capacity of the eels to conquer the current. The tests were also carried out in different light conditions to establish the obstructive influence of light on migration. The investigation was carried out in June, 1950, at the Swedish Salmon and Trout Association's laboratory at Håstad Mölla, with the kind co-operation of its Director, PH. WOLF, and the Fishery Assistant, OLOF BJÖRKLUND.

The experimental apparatus can be described as an »eel ladder». It consisted of four basins connected by channels (see Fig. 1). The basins were made of wooden boxes measuring 45 cm in length, and 30 cm in width and depth. The channels were 120 cm long, their inside width was 8 cm and inner depth 9 cm. Their inner surfaces were planed. Their mouths were 20 cm above the bottom of the basins. The depth of water in the channels varied from 3 cm to 5 cm. The rate of flow was regulated partly by varying the water supply and partly by changing the angle of the channels. This last method enabled us to increase the rate of flow from one channel to another. The rate of flow was determined by floating a wood shaving down a channel several times, and registering its speed over the distance on a stop-watch. The method entailed a certain degree of error, as the current was not uniform in the

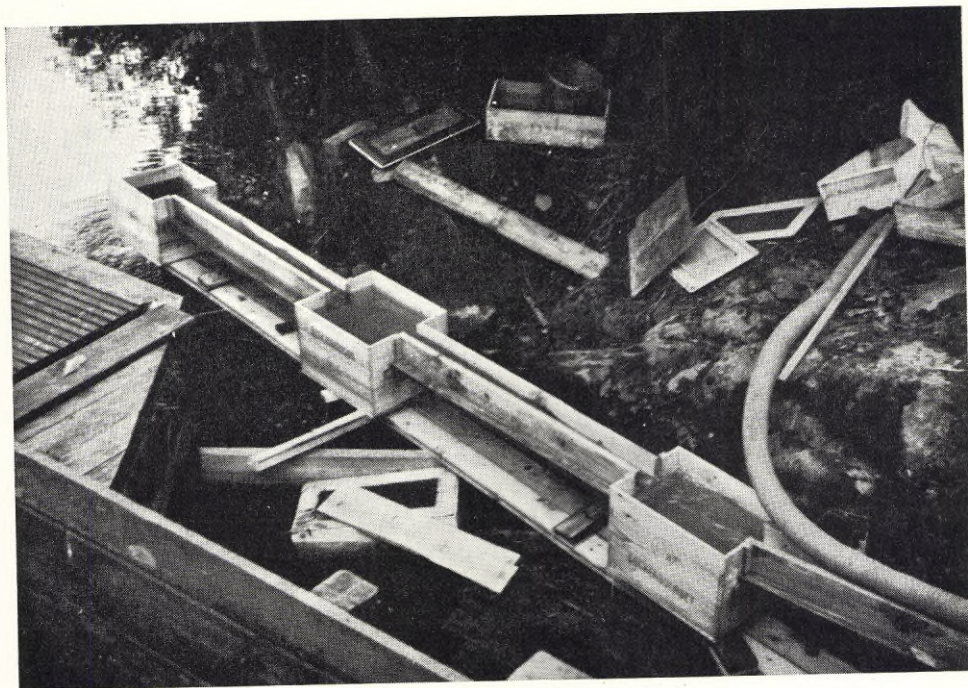


Fig. 1. Experimental apparatus for the investigation of the upstream migration of the eel. On being placed in the basin on the left of the picture, the eel could travel upstream from basin to basin.

whole cross section but stronger in the middle than at the sides and bottom. The depth of water was, however, relatively slight, so that variations in the rate of flow cannot have been particularly large. The experiments showed that the eel did not rest for periods at the bottom or sides as they made their way up a channel, but travelled the whole distance without a break. If the eel was not strong enough to work its way up the whole length of the channel it was washed back into the basin below as soon as it lost speed. The eel did not, then, take advantage of the weaker current at the bottom and sides of the channel. Therefore the method employed in determining the rate of flow cannot have had any great adverse effect on the accuracy of the results. The experimental material consisted of some 100 eels, between 7 cm and 30 cm in length, which had been caught at Höjasmölla in the River Kävlingeån, at a point about 10 km from the river's mouth in Öresund.

With the help of the apparatus described above, four different experiments were carried out under varying light, temperature and current conditions. At the start of each experiment, the eels were placed in the bottom basin, and then made their way up against the current through the channels and resting basins. The varied rates of flow caused a natural division of the eels into

the three following length groups: 7—10 cm, 10—15 cm and 15—30 cm. In the experiment at the lowest water temperature, the last group included only eels measuring 20 to 30 cm. The exact length of each eel used in the experiments was not measured, as the procedure would have been too cumbersome. At the end of each experiment the eels were caught one by one in a device consisting of a frame, with a handle, over which a fine net had been stretched. The eels' length was gauged by comparison with the length of edge of the frame. The error in this method of measurement cannot have exceeded 1 cm. This error can, of course, have led to some eels being classed to the wrong length group. In a general assessment of the eels' reactions to different external factors, however, this degree of inaccuracy cannot be of any significance. Water from the River Kävlingeån was used for experiments in which the water temperature was 19.8° C. The water for experiments at lower water temperatures was taken from the hatchery at Håstad Mölla. The oxygen content of the water was sufficient in both cases.

Experiment No. 1. The experiment took place between 9 a.m. and 3 p.m., the apparatus being placed in the shade so that no direct sunlight had access. The water temperature was 19.8° C., a temperature shown to be favourable to the upstream migration of eels by observations made at the elver-catching station at Trollhättan, among others. As can be seen in Table 1, despite the optimal temperature during the six hour experiment, only 15 of a total of 88 eels had left the basin in which they had been placed. The influence of light on the upstream movement of eels can best be seen by comparing the results of this experiment with those of the subsequent test, in which the only change in conditions was the blacking-out of basins and channels. Thus, in light, only 17 % of the whole number made their way upstream from the lowest basin, whereas after the black-out not less than 94 % travelled upstream. Further, in the first experiment only small eels left the relative darkness of the first basin to make their way up through the lighter communicating channel. This points to the fact that the larger eels are more sensitive to light. The relative insensitivity of elvers to light is also indicated by the fact that they sometimes try to work their way up the leaks from the dams in daylight.

Of the elvers which had travelled upstream in Experiment No. 1, even the smallest, or those measuring up to 10 cm, had been able to make their way against a current of 0.6 metres per second. When the rate of flow was increased to 1.5 metres per second, the resistance became too strong for both these and somewhat larger elvers. Only a 16 cm long eel could make headway against this current.

Experiment No. 2. This experiment took place between 4 p.m. and 10 p.m., and the whole apparatus was, as mentioned above, well-screened against light. Temperature and current conditions were the same as in the preceding experiment. As the black-out caused practically all the eels to leave the

Table 1. Results of experiments to investigate the effect of light, water temperature and rate of flow on the upstream movement of eels measuring 7 cm to 30 cm. The movement took place from the basin with the lowest number to that with the highest. The distribution recorded was registered at the end of each experiment.

	Experiment No. 1	Experiment No. 2	Experiment No. 3		Experiment No. 4	
Duration of experiment, in hours	6	6	12		7	
Light conditions	shade	dark	dark		dark	
Water temperature, °C.	19.8	19.8	19.8		12.0	
Distribution in basin No. 1,						
number of eels	73	5	1		61	
length in cm	7-30	7-15	7		7-30	
Rate of flow in channel No. 1,						
metres per second	0.4	0.4	0.4		0.4	
Distribution in basin No. 2,						
number of eels	6	7	30	1	3	1
length in cm	7-15	7-15	7-10	17	10-15	20
Rate of flow in channel No. 2,						
metres per second	0.6	0.6	0.9		0.7	
Distribution in basin No. 3,						
number of eels	8	63	37		4	
length in cm	7-15	7-15	10-15		20-30	
Rate of flow in channel No. 3,						
metres per second	1.5	1.5	1.3		1.2	
Distribution in basin No. 4,						
number of eels	1	10	1	25	3	
length in cm	16	15-30	12	15-30	20-30	

bottom basin, this experiment gives a good picture of the distribution of the material, heterogenous as regards size, into groups on the basis of the varying current conditions in the apparatus. A rate of flow of 0.6 metres per second did not greatly impede the elvers' upstream movement, whereas a rate of 1.5 metres per second stopped all upstream movement of eels measuring less than 15 cm.

Experiment No. 3. The experiment took place between 8 p.m. and 8 a.m. The apparatus was not covered but the night was dark and therefore favourable to movement. The water temperature was the same as in the preceding experiments, 19.8° C. At the end of the experiment 99 % of the eels had left the bottom basin. The rate of flow in the second channel had, for this experiment, been increased to 0.9 metres per second. This current was too strong for elvers under 10 cm in length. It did not appear to cause any great difficulty to elvers measuring from 10 to 15 cm, as a large number belonging to this length group had moved up to basin No. 3. Only one eel under 15 cm in length had been able to make its way against the current of 1.3 metres per second in the third channel.

Experiment No. 4. The experiment took place between midnight and 7 a.m. The apparatus was completely blacked-out and the water temperature was 12° C. Before the experiment started the eels were transferred successively, during a period of several hours, from a water temperature of 19.8° C. to 12.0° C. During the experiment only 15 % of the total stock of eels left the basin in which they had been placed. None of the eels which moved upstream belonged to the smallest length group. Three specimens, which reached basin No. 2, measured 10—15 cm. The rest of the eels which had travelled upstream — 11 % of the experimental material — were 20 cm or more in length. Three eels belonging to this last length group had managed to work their way against the strongest current which, in this experiment, had a speed of 1.2 metres per second. The experiment illustrates well the significance of the temperature factor in the upstream migration of eels. It does not only show that a low water temperature is obstructive to their activity on the whole, but also that this effect is greater on the weaker elvers than on larger eels.

In connection with the experiments described above, another method was used to investigate the effect of current on the eel's upstream movement. In this method a rotating aquarium (see Fig. 2) was employed. It was constructed by PH. WOLF on an American idea. The round, glass aquarium has an inner diameter of 28 cm, and is fixed on a large, horizontal disc which is rotated by a small engine by means of a transmitter. In the centre of the aquarium there is a cylindrical inset, 20 cm in diameter. The inset is not attached to and does not rotate with the aquarium. A strip of rubber prevents the eels from getting underneath the inset. The water in the 4 cm wide channel between the walls of the aquarium and the inset starts moving as the aquarium rotates, and after a while reaches about the same speed. The speed of the water, which of course decreases towards the centre, was calculated at a distance of 1 cm from the aquarium wall, as the eels placed in it showed a clear tendency to remain near the outer wall as the aquarium was rotated. To a certain degree the eels swam against the current when the aquarium rotated. Their reaction was, however, not uniform; quite a number of eels drifted apathetically with the current. Eels measuring between 15 and 30 cm, in particular, showed no great inclination to make their way against the stream. To ensure accurate observations the experiments had to be carried out in relatively good light. The fact that the larger eels — already proved to be more sensitive to light than elvers — were more disorientated than the elvers can probably be blamed on the light. The rotation of the aquarium can also have caused certain irritating sensations of vision and pressure. I describe some of these tests — despite the weaknesses of the method, mentioned above — as two of the experiments with small elvers gave relatively accurate results. It is possible, then, that the method is better suited to experiments with species of fish less sensitive to light than the eel. The water

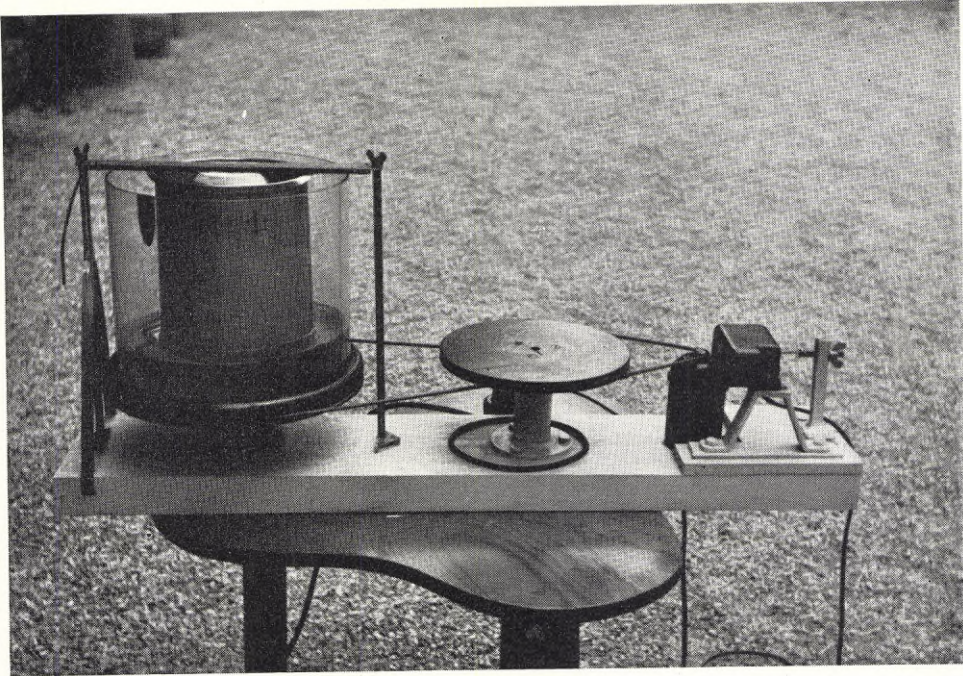


Fig. 2. The rotating aquarium used in experiments Nos. 5 and 6.

temperature in the aquarium was about 20° C. in all the experiments. Halts were called during the experiments to ensure that no inaccuracy would be caused by the fatigue of the eels.

Experiment No. 5. An elver measuring 8 cm in length could make its way against a current of 0.3 metres per second for several minutes at a time. If the current was increased to 0.4 metres per second the elver was swept back after a minute or so by the stream, but still tried time and again to swim against it. At a water speed of 0.5 metres per second the elver could make headway against the current for only 10 or 20 seconds, and at 0.6 metres per second it could make no headway at all.

Experiment No. 6. A 13 cm long elver had the strength to hold its own for a few minutes against a current of 0.5 metres per second. At 0.6 metres per second the elver swam tenaciously against the current but was swept steadily backwards. When the flow was increased to 0.7 metres per second the elver lost its balance after only 10 or 20 seconds. At 0.8 metres per second it was carried back at once by the stream.

Discussion

In summarising the results of the various experiments, it can be said that the upstream movement of the eel is greatly affected by the prevailing

light, temperature and current conditions. The effect of these factors is, however, relative to the size of the eel. Light appears to have a marked obstructive effect on the movement of larger eels, whereas the smaller elvers do, to a certain extent, make their way upstream in light. On the other hand, the activity of elvers is decreased by low water temperatures. In this regard larger eels show less sensitivity than elvers. At a water temperature of 20° C., the maximum rate of flow against which eels measuring 7—10 cm can make headway lies between 0.6 and 0.9 metres per second; for eels measuring 10—15 cm the maximum current is between 0.9 and 1.3 metres per second. Larger eels can make headway against a water speed of 1.5 metres per second or more. In a preparatory experiment some eels measuring 30 cm escaped through a supply pipe in which the current was appreciably faster than 1.5 metres per second. It should be borne in mind that the limit values given refer to experiments in which the eels had to travel a distance of 1.2 m if their activity was to be registered. Over a shorter distance they would have been able to make headway against somewhat faster currents than those shown by the experiments. The figures for the elvers' capacity against different rates of flow in the rotating aquarium are somewhat lower than the limit values given above. These limit values are based on experiments Nos. 2 and 3, in which irrelevant external factors were eliminated to a greater degree than in Nos. 5 and 6. As the corresponding figures in both experimental groups are of the same order, the results of the last two experiments should serve to confirm the accuracy of the results of the preceding experiments.

Number of eggs in different populations of whitefish (*Coregonus*)

By HENDRIK TOOTS

Below I present a few figures on the amount of roe in some populations of small whitefish in various lakes in the north of Sweden. The figures have been collected during the spawning-time of whitefish with fully developed but not running roe. The names of the various species of whitefish are from G. SVÄRDSON's preliminary classification of different Swedish species of whitefish not yet published.

Some time before the investigation the whitefish were preserved in 4 % formalin. In order to establish the difference between fresh and preserved fish, the length and weight of 97 whitefish were ascertained before and about four months after preservation. It appeared that, on the whole, preserved whitefish had shrunk somewhat but increased in weight. On the average the contraction per 10 cm was 0.95 mm, and the increase in weight per 100 g 8.6 g. The increase in weight per 100 g in a male was 8.4 g and in a female 8.8 g, so there is no essential difference between males and females, and we may suppose that the weight of the roe in preservation increases to the same extent as the weight of the fish, and that the relation of weight between roe and fish is the same in preserved fish as in fresh.

The lakes, in which the material was collected (Fig. 1), are all more or less oligotrophic in type but differ in various respects. Figures from the lakes in question will be found in Table 1, where also all the whitefish tested are tabulated. The other species of fish in these lakes are, as a rule, pike, perch, burbot, roach, trout, grayling and others, but we have no exact knowledge of the density of their populations in the various lakes.

The average values of the roe calculations will be found in Table 2, from which we also see that the populations of the smallest whitefish have the lowest average age in the spawning stocks. Thus, the population in Lake Vojmsjön has an average length of 99 mm and an average age of 2.5 years, whereas population I in Lake Idsjön has a length of 309 mm and an age of 4.2 years. Closer investigations of population I in Lake Idsjön have proved that the average age varies a little from one year to the other, but still keeps within certain margins.

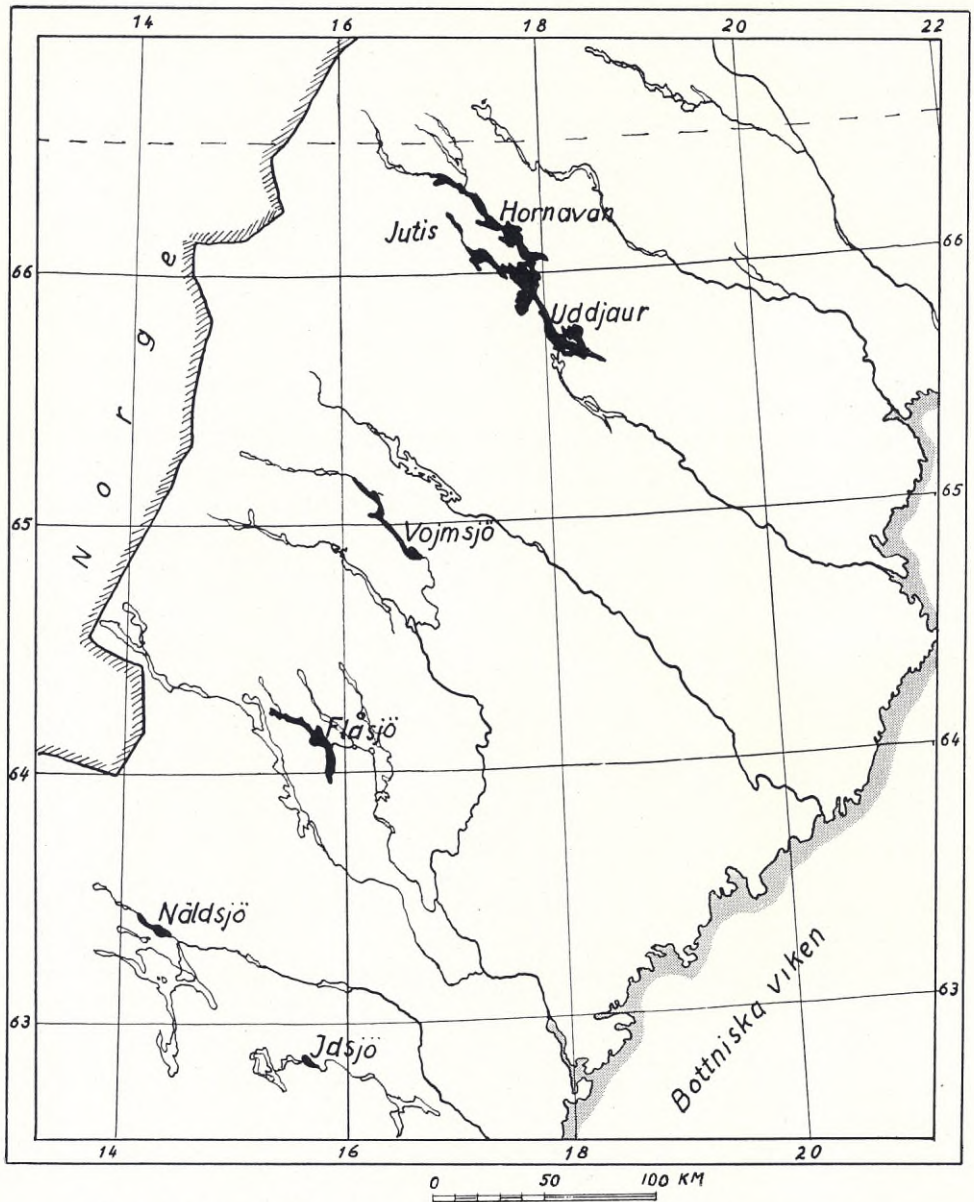


Fig. 1. Position of the lakes from which the whitefish samples were taken.

The roe counted in percent of the weight of the fish varies considerably in different populations. Thus the roe of whitefish in Lake Hornavan is on an average 18.9 per cent of the weight of the fish, as compared with 7.7 per cent in Lake Vojmsjön. The individually highest percentage of roe also occurred in Lake Hornavan, 27.8 ‰, and the lowest in Lake Vojmsjön, only 6 ‰.

Table 1. Data on the lakes from which the material investigated was taken. ⊕ denotes the species of whitefish whose number of eggs has been investigated.

Name and position of lake		Area in sq km	Depth in m	Height above sea in m	Storsik	Älvsik	Blåsik	Aspsik
Idsjön	Jämtland	12.3	under 50	261	+	⊕	⊕	—
Näldsjön	»	41.9	» 50	302	+	⊕	+	—
Flåsjön	»	111.6	50—100	265	+	⊕	?	—
Vojmsjön	Lapland	77.7	over 100	413	+	—	⊕	+
Uddjaur	»	238.3	50—100	419	+	—	⊕	+
Hornavan	»	251.1	appr. 200	425	+	—	⊕	+
Jutissjön	»	8.2	under 50	432	⊕	—	?	?

As far as the amount of roe in different populations is concerned, the investigation has proved that the total amount of roe is, on an average, larger in populations in which the size of the fish is larger (Fig. 2). Thus *blåsik* (blue whitefish) in Lake Idsjön with a body length of 30.9 cm have 5,784 grains of roe, whereas the population in Lake Vojmsjön with an average length of 9.9 cm have only an average of 300 grains of roe.

The *älvsik* (river whitefish) in Lake Näldsjön with an average length of 20.8 cm have 2,434 grains of roe, whereas the population in Lake Flåsjön with an average length of 14.7 cm have 703 grains of roe.

Generally, the same rule applies within single populations too; for instance in *blåsik* in Lake Idsjön with an average length of 27.2 and 33.0 cm, re-

Table 2. Average number of eggs, relative amount of eggs per mm in the different populations.

Species of whitefish	Name of lake	Number of fish studied		Length in mm	Weight in g	Age	Number of gillrakers	Total number of eggs	Spawn weight in g	Spawn in % of fish weight	Number of eggs per 1 g	Number of eggs per 100 g of fish weight	Number of eggs per 1 cm fish
<i>Blåsik</i>	Idsjön I	12	309	246.3	4.2	35.1	5784	40.4	16.2	149	2392	187.2	
	Hornavan	18	149	22.6	3.5	33.9	928	4.3	18.9	215	4116	62.1	
	Uddjaur	4	137	18.7	2.8	35.7	825	3.3	17.5	252	4392	59.8	
	Vojmsjön	4	99	5.4	2.5	38.0	300	0.42	7.7	766	5758	30.4	
<i>Älvsik</i>	Näldsjön	14	208	70.3	3.8	31.0	2434	10.9	15.3	240	3595	115.0	
	Idsjön II	20	149	23.7	3.9	28.9	1060	2.2	11.1	484	4545	71.0	
<i>Storsik</i>	Flåsjön	10	147	21.5	3.1	30.0	703	2.6	11.9	273	3296	47.6	
	Jutissjön	8	192	62.9	4.0	20.0	2442	10.6	16.5	241	3834	119.4	

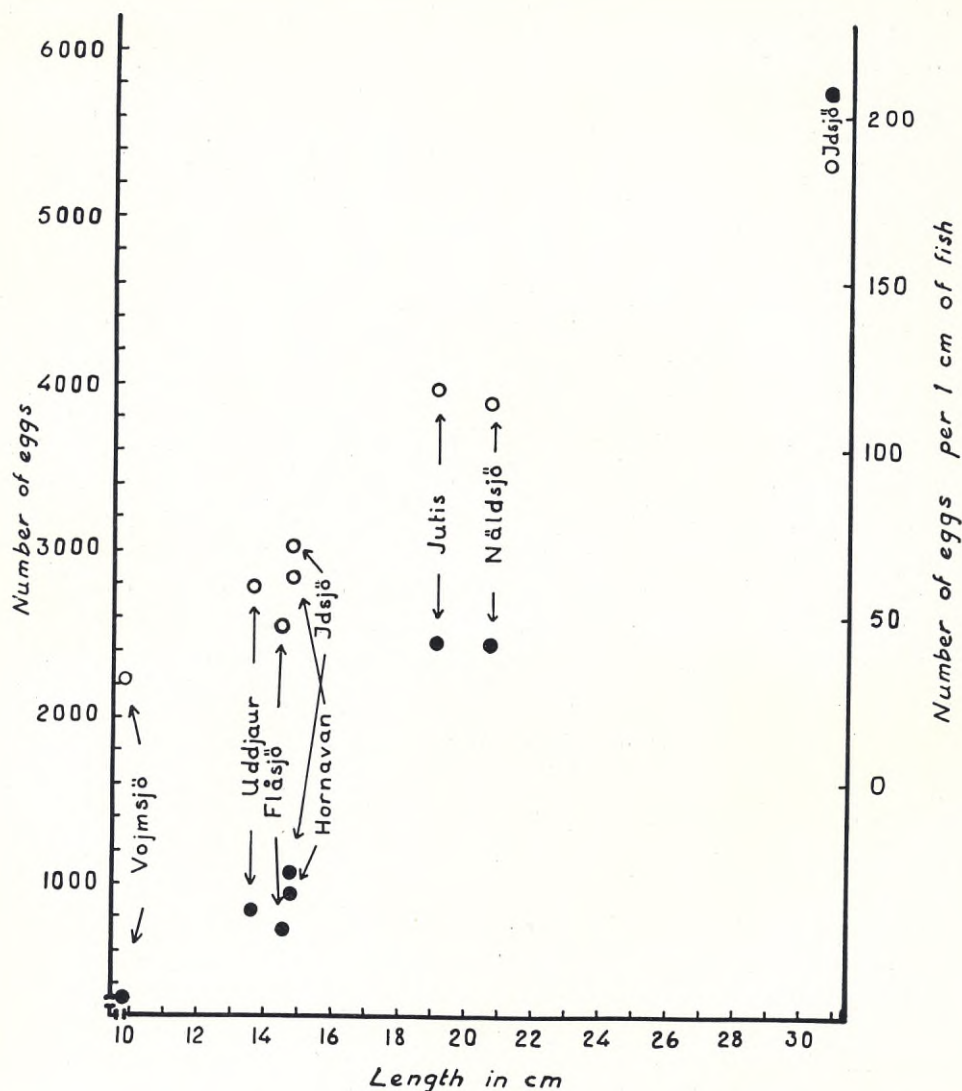


Fig. 2. Relation between number of eggs and length of fish ●, and relation between number of eggs per 1 cm of fish and length of fish ○.

spectively, the amount of roe varies from 4,896 to 8,462 grains; in *älvsik* (river whitefish) in Lake Nälidsjön from 1,491 grains at 18.3 cm to 3,106 grains at 25.0 cm; in *storsik* (large whitefish) in Lake Jutissjön from 1,366 grains at 16.4 cm to 4,826 grains at 24.2 cm, etc. Thus a positive correlation between length of body and amount of roe is evident, both between and within different populations.

The diagram (Fig. 2) shows, however, that the amount of roe does not always increase in proportion to the size of the fish. Thus, for instance,

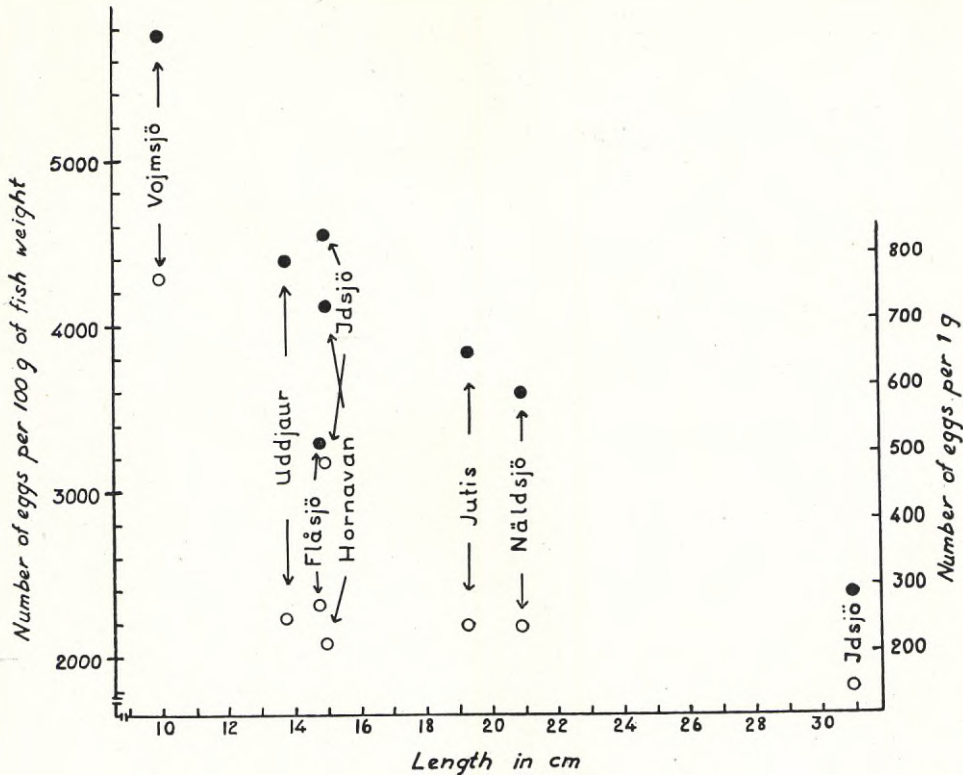


Fig. 3. Relation between number of eggs per 100 g of fish weight ●, and relation between number of eggs per 1 g of egg weight and length of fish ○.

whitefish in Lake Flåsjön with an average length of 14.7 cm have an average of only 703 grains of roe, whereas whitefish in Lake Uddjaur with a length of 13.7 cm have 825 grains; whitefish in Lake Jutisjön measuring 19.2 cm in length have 2,442 grains of roe, whereas whitefish in Lake Nåldsjön with a length of 20.8 cm have only 2,434 grains. Whitefish from Lake Hornavan and *blåsik* from Lake Idsjön are of the same length, but the former have 928 grains of roe against the 1,060 of the latter.

These slight divergences may be due partly to the scantiness of the material investigated, partly to the fact that the biological environment may be different in different lakes, so that — by selection — different amounts of roe may have been formed in different populations. Owing to our insufficient knowledge of the number of fish in the populations, and the competition from other species of fish in the various waters, it is at present impossible to suggest a definite explanation of this problem.

The diagram shows, too, the amount of roe per 1 cm of length of fish.

The diagram in Fig. 3 shows the amount of roe in various populations per 100 g of fish and the number of grains per 1 g. It appears that if we count

the amount of roe per 100 g of the weight of fish, there is a negative correlation between the size of the fish and the amount of roe, *i.e.* populations with large-sized fish produce proportionately considerably less roe than populations consisting of small-sized fish.

The *älvsik* in Lake Vojmsjön have the highest relative amount of roe, 5,758 grains, whereas the population of the same species of whitefish in Lake Idsjön have the lowest amount, 2,392 grains. The average lengths were 9.9 cm and 30.9 cm, respectively.

It was not possible to measure the size of the grains of roe, as they had been partly flattened in the ovary in preservation and so could not give reliable values. The relative size of the eggs in the different populations should, however, appear in the amount of eggs per 1 g and — as can be seen — there is a positive correlation between the size of the fish and the size of the eggs. As, for instance, the amount of eggs per 1 g in the Vojmsjön population is 766, as compared with 149 in the Idsjön population, the eggs of the former population must be considerably smaller.

The divergences found in this material are — as is also true of the egg-number — probably due in part to different conditions of heredity in the population of whitefish.

The result of the investigations may be summarized thus:

- 1) The total number of eggs is larger in populations of large-sized whitefish,
- 2) The relative number of eggs is larger in populations of small-sized whitefish,
- 3) Large whitefish have, on an average, larger eggs than small white-fish.

Plankton Mortality in the Northern Baltic caused by a parasitic water-mould

By STEN VALLIN

At the beginning of August 1950 it was reported that herring fishermen in the Botten Sea, off Sundsvall, had found their nets to be clogged with a sticky substance. When the tackle was taken out of the water the substance soon began to rot and smell. It was suspected that its cause might be industrial pollution from cellulose plants. Samples of the material scraped off the nets, some treated with formalin, were however found to consist of dead plankton crustaceans. A single species of copepod — *Eurytemora hirundoides* (NORDQUIST) — formed almost 100 % of the substance. They had been killed by a parasitic water mould (*Saprolegniaceae*). Only very few other crustaceans were found in the samples, none of which had been attacked by the fungus. Of the dead *Eurytemora* there usually remained only the skeleton, filled with the mould's oogonia and antheridia on their hyphae (Fig. 1). The primary infective stage with well developed mycelium with zoospore formation was found more rarely in these samples (Fig. 2).

A week later a *netted sample* of plankton was taken at Lörudden, off Sundsvall. This contained comparatively few *Eurytemora* with the mould most of it consisted of the following species of plankton, free of mould:

Eurytemora hirundoides, NORDQUIST

Acartia bifilosa, GIESBRECHT

Limnocalanus grimaldi, (DE GUERNE)

Bosmina maritima, MÜLLER

Evadne nordmanni, LOVÉN

The following information on the death of the plankton was given. It was first reported from fishing grounds east of the island of Alnö, off Sundsvall, at the beginning of August. Fishermen found such large quantities of dead *Eurytemora* on their nets that they could easily scrape it off by the quart. At the same time the local fishery assistant stated that the sea water in wide areas was made turbid by a lot of »small dead white eggs», what instead of that must have been the killed copepods. Within a few days the same phenomenon was reported from other fishing waters, from Tyndersö—

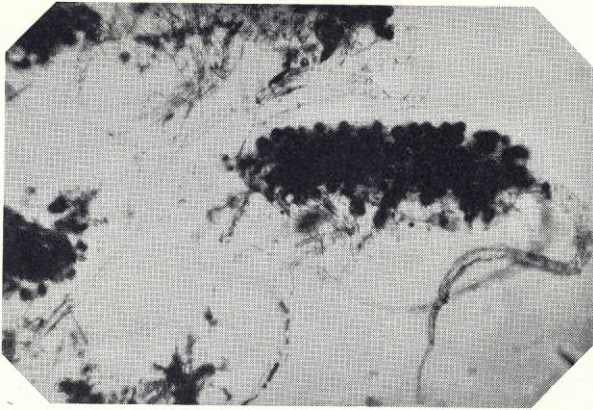


Fig. 1. *Eurytemora* skeletons filled with oogonia and antheridia. 60X.

Barsviken in the north down to Hundgrundet, south of Brämö—Brämökalv, in the south. The area, then, stretched for some 70 km in the outer skerries off Sundsvall.

I would like to draw attention to the following points as regards the mould itself. It is clearly a true animal parasite and, on the evidence of observations to date, specifically related to *Eurytemora hirundoides* as host. According to the literature available, the following *Saprolegniaceae* have been observed as animal parasites in the Scandinavian countries:

Aphanomyces astaci, SCHIKORA, — the common crayfish's disease fungus. A related form — *Leptolegnia caudata*, DE BARY — was observed in Furusö in Denmark by MÜLLER as early as the eighteen-sixties. It was reported again later in the same lake by WESENBERG-LUND and H. E. PETERSEN. It attacks and has on occasions almost entirely destroyed the stock of *Leptodora hyalina* in the lake. Further, a third form, *Pythium daphnidarum*, PETERSEN, belonging to another type of these fungi, has also been reported in Denmark, Its hosts are *Daphnia cucullata* and *D. hyalina*, but it does not seem to have caused any widespread mortality.

The species of mould in question shows great similarity to both *Aphanomyces astaci* and *Leptolegnia caudata*. The mycelium shows similar development but is appreciably larger than that of the *Aphanomyces astaci*. The spore formation resembles most closely that of *Leptolegnia*, COKER p. 158. Living zoospores were observed. The oogonia, antheridia and fertilization also closely resemble those of the *Leptolegnia caudata*. In the known parasitic forms of these two genera, oogonia and antheridia have only occurred sporadically. They have never been observed in natural *Aphanomyces astaci*, and only rarely in cultures (RENNERFELT 1936). The formation of sexual organs is however extremely plentiful in the form of mould in question and,

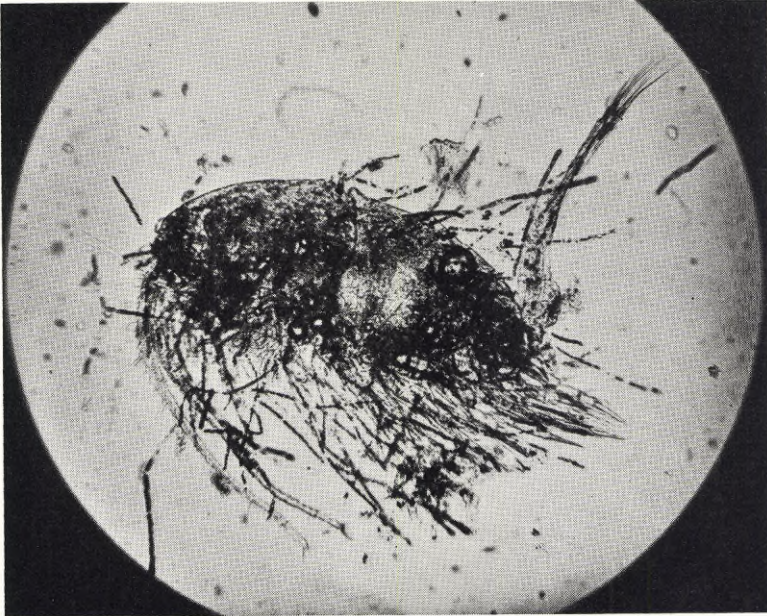


Fig. 2. *Eurytemora* with well-developed mycelium. 75 \times .



Fig. 3. Internal mycelium (out-prepared). 250 \times .



Fig. 4. External mycelium (sporarium) with spore formation. 250 \times .

as I have already pointed out, the empty copepod skeletons are completely filled with, primarily, oogonia.

One might, perhaps, imagine the mould to attack in this way. The zoospores, which abound in the water during an epidemic, probably attack the animal round the mouth. In all probability *Eurytemora* feed by filtering small organisms in the water, in which case the zoospores could easily be accumulated in the mouth regions of the copepod. The mycelium develops from the spores and grows through the soft parts of the crustacean to emerge through the joints, and then spores are formed in the hyphae. When the soft tissues are completely eaten away by the fungus mycelium, and only when nothing but the skeleton of the *Eurytemora* remains, the mould's sexual organs — oogonia and antheridia — are formed. Oogonia in particular fill the entire copepod skeleton, which is then burst open by the mass of fungi (Fig. 1).

A brief preliminary description of the mould includes:

The primary mycelium resembles that of the *Aphanomyces*, but is appreciably larger, 15—20 μ . In the internal parts of the copepod the hyphae are thick and typically branched generally in right angles (Fig. 3), what according

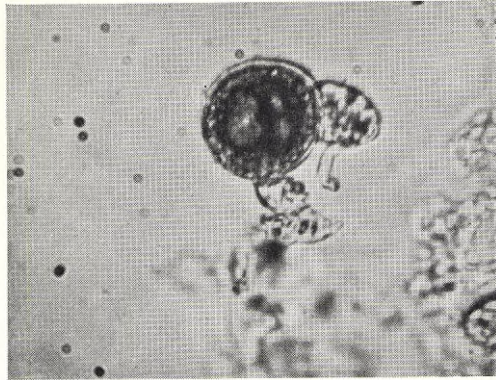


Fig. 5. Antheridium applied to an oogonium. 400 \times .

to PETERSEN is characteristic of *Leptolegnia caudata* in *Leptodora*. Outside the copepod body the hyphae are more elongated and scantily branched (Fig. 2 and 4). The mycelium is more or less filled with a granular plasma, which in the external parts as well as in the internal parts forms zoospores; the spores typically in a single row (Fig. 4 and 7 a—c). In living state the spores in the hyphae are irregularly angled (Fig. 7 c) as in the Fig. 5 a by COKER p. 148; preserved with formalin the spores become a more rounded oval shape (Fig. 4). The sporangium cannot be morphologically distinguished from the other hyphae. The zoospores leave the sporangium one at a time. Massing of spores at their ejection in a cluster as by *Aphanomyces* does not appear to occur. The zoospores are equipped with two cilia, one of them a little longer than the other (Fig. 7 d). The shape of the just discharged zoospores exactly correspond to *Leptolegnia* spores drawn by COKER, his Fig. 5 b—5 h.

Sexual reproduction organs are found in great numbers principally not before spore formation has ceased. The oogonia with a thick membrane on short (100—200 μ) rather thick stems, measure some 40 μ in diameter. There is only one egg with peripheral droplets, first filling the oogonium completely (Fig. 7 e). After copulation a slight space usually forms between the oogonium membrane and the egg. The antheridia are smaller, rounded or pear-shaped with a thin membrane. They are situated terminally on fine stems from their own hyphasystem (Fig. 5, 6 and 7).

The mould's characteristics appear to correspond closely to those of the *Leptolegnia caudata*: A more detailed description cannot be given until material in culture have been subjected to a more thorough examination. Probably it is a new species of the genus *Leptolegnia*. Its specific host appears to be *Eurytemora hirundoides*. An interesting point is that it is found in the brackish waters of the Bottom Sea, where the surface water has a salt content of 4—6 ‰. The literature available at the present time suggests that

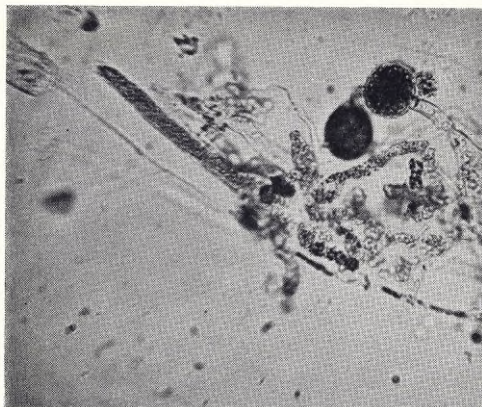


Fig. 6. Mycelium, oogonia and antheridium. 220 \times .

all the submerse animal *Saprolegniaceae* parasites up to now described are freshwater forms.

On the basis of our present knowledge, *Eurytemora hirundoides* seems to be the only host (although hyphae, probably belonging to the same species of mould, once have been observed in *Acartia bifilosa*), so this copepod's occurrence and frequency is of particular interest. HESSLE and VALLIN (1934), in a paper on the Plankton in the Baltic, have established the fact that, during the warmer months of the year, this *Eurytemora* species is the most common Copepod in the surface waters of both the Botten Sea and the skerry area of the central Baltic. From July to September it normally constitutes more than 50 ‰, and often up to 80—90 ‰, of all the copepods in the samples taken in these waters. From 1,000 to 6,000 individuals have been found per cubic meter of water in these areas. It decreases in numbers and significance further north in the Botten Sea and south of the Åland Sea towards the open Baltic. On the basis of these investigations, the salt content of the water should be between 3 ‰ and 6.5 ‰ if large-scale production of this *Eurytemora* species is to take place. On the whole, however, *Eurytemora* can be regarded as the inner Baltic's most common and widespread copepod during the warm months of the year.

Eurytemora can, without doubt, be considered an important food for, above all *Clupea harengus*, and also for other fish that feed on plankton. Widespread death of this copepod, such as that reported from the Botten Sea off Sundsvall in 1950, could involve a fall in food supplies, at least temporarily, of a size that would cause a decrease in the numbers of herrings in the areas affected. A more palpable inconvenience to fishery, however, is the clogging of nets with dead plankton, described above. It is also possible that it damages the nets by making the twine brittle. The herrings caught are also dirtied by the substance and must be rinsed after being shaken. It is probable, however, that these inconveniences to fishery are relatively temporary. It

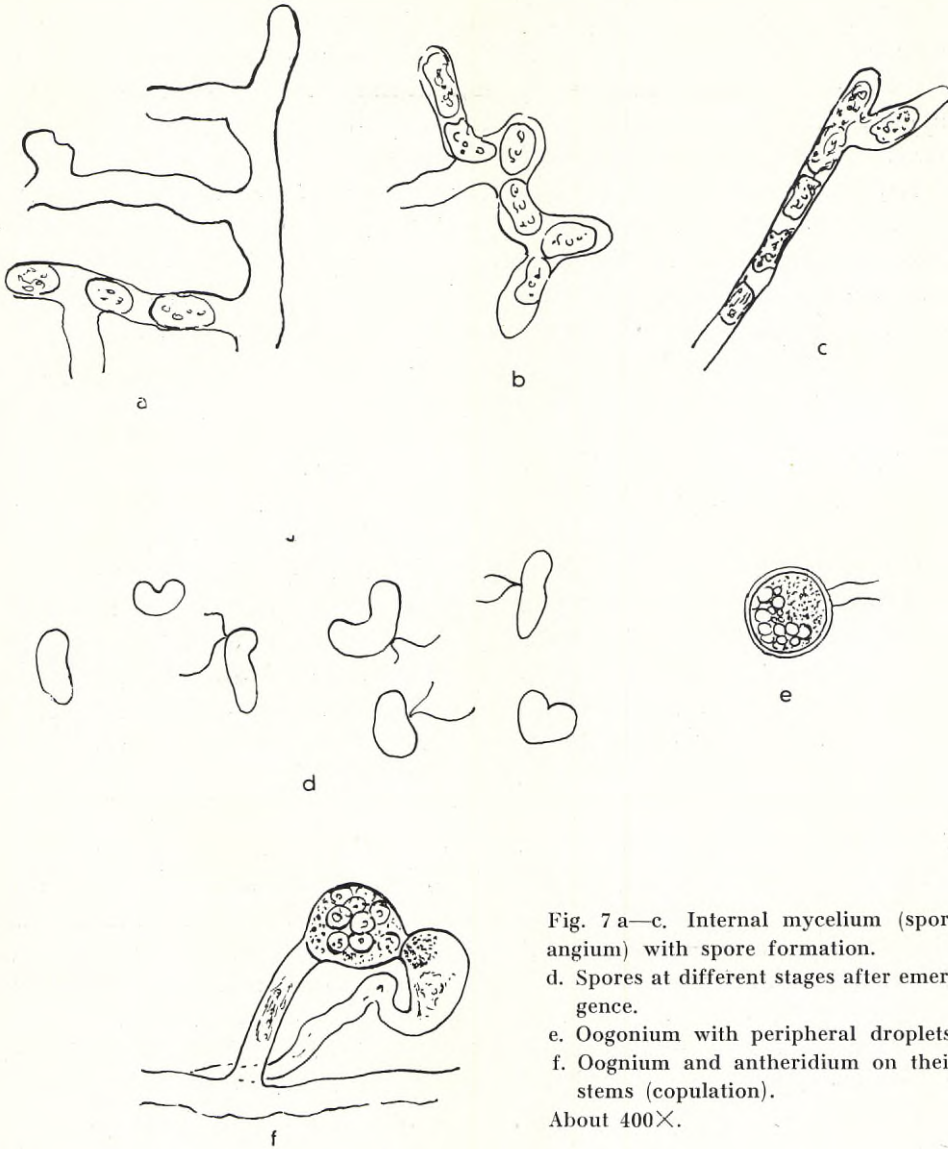


Fig. 7 a—c. Internal mycelium (sporangium) with spore formation.

d. Spores at different stages after emergence.

e. Oogonium with peripheral droplets.

f. Oogonium and antheridium on their stems (copulation).

About 400X.

would appear advisable to discontinue fishing for short periods when the water contains a high proportion of these dead animals.

The density of the stock of *Eurytemora* during the summer in all parts of the Botten Sea entails an obvious danger of the fungus spreading. From the middle of August to the end of the month in 1950 the State Fishery Inspection boat took samples at different points in this area. These samples were netted, as a rule vertically, from a depth of 25—0 m. The stations at

which *Eurytemora* were found to be attacked by the mould have been marked + in the diagram (Fig. 8), those at which no mould was found are marked —. The diagram shows, then, that in August the mould had spread along the Swedish coast from Umeå in the north to Söderhamn in the south. Off Sundsvall it was also found right out in open waters.

Reports received from fishermen of the presence en masse of dead *Eurytemora*, and of the difficulties caused to fishing by nets being clogged, have come primarily from the Sundsvall area (Fig. 8: 1.), in a lesser degree from waters off Hudiksvall—Söderhamn (Fig. 8: 2) and off Örnsköldsvik (Fig. 8: 3). Reports have also been received to the effect that the planktonmortality has been observed on the Finnish coast north of Åland.

Where the mould came from, and why it appeared first in the Bay of Sundsvall, are questions to which we have no answer. There is no reason to connect the phenomenon with pollution from industries or towns, as the parasite is bound to a specific host. Factors which may have favoured the rapid growth of the mould are, first, the influx of fresh water from the Indal River during the late summer being unusually strong for the season and, secondly, a period of calm, warm weather with exceptionally high temperatures in the surface water — up to 20° C. at the Ulvö Islands in the open Botten Sea and 23° C. in the archipelago. Probably high water temperature favours the mould. The optimum temperature for the related crayfish disease fungus is 20—25° C., though it can also be virulent in the winter.

In the summer 1951 the *Eurytemora* mortality was not reported by the fishermen before the last days of August from the archipelago off Härnösand and from the aereas east of Alnö off Sundsvall. Plankton samples netted on the 9 and the 23 September contained affected *Eurytemora*. Also some individuals of affected *Bosmina maritima* were found in these samples but the examination showed in this case another type of parasitic water-mould's probably a *Pythium spec.* In one sample from the 9 September netted in a rather closed bay of Alnö the number of surviving *Eurytemora* only was 13 % of all the copepods, normally this figure at this time being about 80 %. The appearance of the mould in the plankton about four weeks later and the plankton destruction being not at all so widespread as in the year 1950 may be referred to the rather cold summer in the year 1951, the surface temperature in the beginning of September being only 13° C. off Sundsvall.

Finally I would like to point out that the *Eurytemora* mortality can hardly be expected to cause any »catastrophe» for herring fishery in the areas affected. There can be no danger of the mould directly attacking herring or any other fish. But it may well lead to a temporary decrease in catches and it is an obstacle to fishing. However the plankton mortality is a phenomenon serious enough to fishing and the possibility of its spreading to other areas

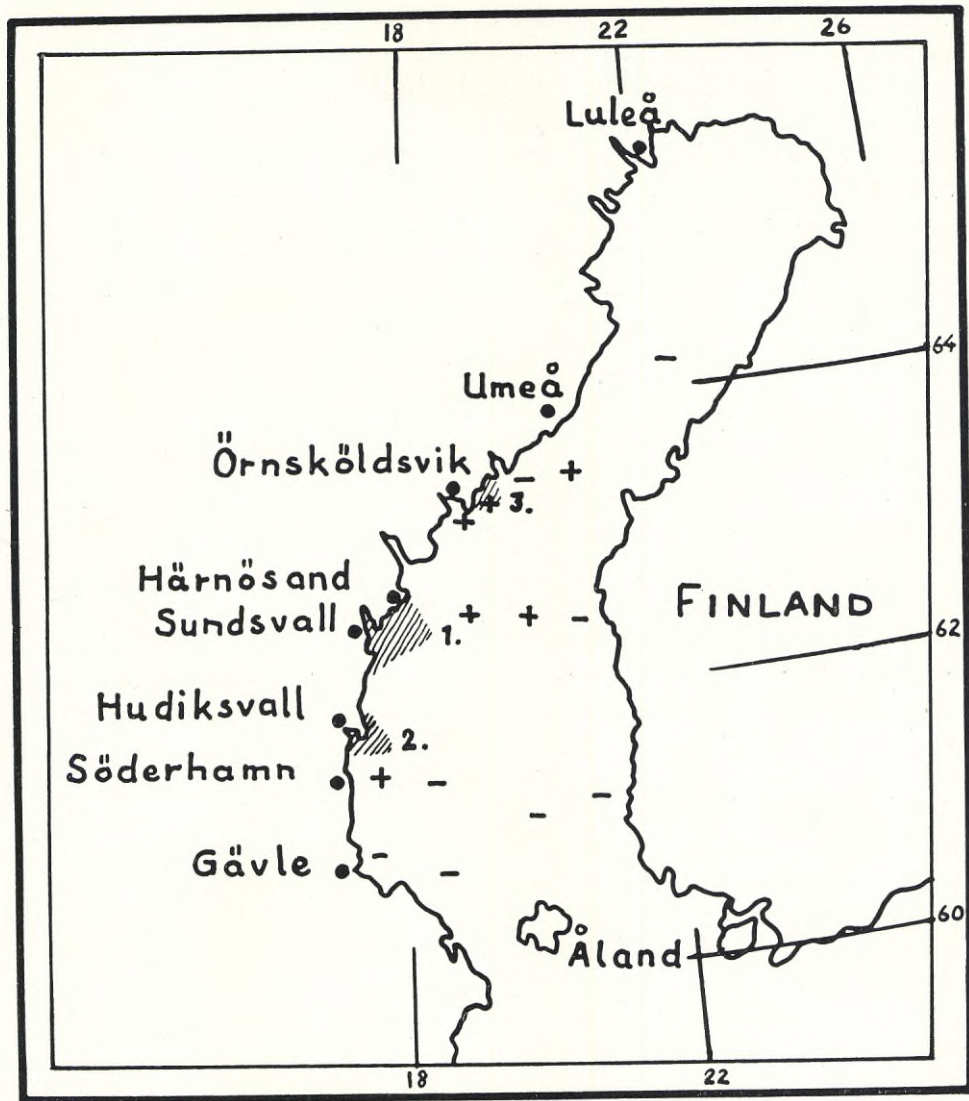


Fig. 8. Distribution of parasitic water mould in *Eurytemora* during August 1950.

/// Areas with difficulties in herring fishery caused by nets being clogged with dead *Eurytemora*.

+ *Eurytemora* attacked by the mould was found in plankton samples.

- The mould was not found in the samples.

of the Baltic ought to be watched carefully. Unfortunately there are no preventative measures which might prevent the spreading of the fungus.

The observations made in the years 1950 and 1951 indicate, that we may expect this plankton mortality to appear in the northern Baltic in the coming years too and then more intense and widespread in years with specially warm summers.

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The Role played by *Didymosphenia geminata* (LYNGBYE) in Clogging Gill Nets

By STEN VALLIN

Pollution of rivers and lakes in Sweden often causes nets to be dirtied, a fact which obstructs fishing and, indeed, at times renders it quite impossible. It can be caused directly by waste products such as wood fibres from the paper industry or, more seldom, from the textile industry. It is, however, more often caused indirectly by drifting tufts of mycetic fungi — *Sphaerotilus*, *Fusarium* and *Leptomitus* — in waters polluted by drains containing organic matter, — from towns and villages, sulphite works, sugar refineries, dairies, etc. High production of certain thread-like cyanophyceae — *Oscillatoria Agardhi* in particular — has caused serious clogging of nets in some lakes, especially in Roxen in 1943.

The waste water from iron works, which is acid and has a high iron content, can also cause clogging of fishing nets. In the water the iron precipitates in clumps from the iron hydroxide, often forming large quantities of thread-shaped iron bacteria — *Leptotrix* sp. This iron deposit fastens on the fine threads in the nets, in this way decreasing their catching capacity appreciably as well as lessening their durability. This clogging of nets has been reported from the coast, as well as from some rivers and inland lakes.

Obstructive clogging of gill nets can, however, occur in lakes and rivers which are not recipients of waste water. In our eutrophic lakes on plains the production of phyto-plankton is sometimes so high that clogging of nets renders fishing impossible, though as a rule only for short periods. This is not seldom caused by various *Melosira* species which reach high production immediately after the spring circulation, and sometimes also during the late autumn.

Further, algae causing »water-bloom» such as *Microcystis* sp., *Anabaena* sp. and, in two lakes, *Gloeotrichia echinulata*, have temporarily made fishing difficult during the summer and autumn by clogging nets.

The most conspicuous agent in the clogging of fishing nets in unpolluted waters is our largest stalked Diatom — *Didymosphenia geminata* (LYNGB.) M. SCHMIDT (Figs. 1 and 2). Its strong, branched stalks grow like white felt on rocks and stones in the falls and rapids in many rivers of Northern

Sweden, and in the surf zone of mountain lakes. It is also common in our two great southern lakes — Vättern and Vänern — where it also grows in the surf zone, both on exposed shores and out in the open lake where rocks rise to the surface. At high water in the rivers and in storms over the lakes it is torn from the rocks. These loose stalks form strong, white tufts resembling cotton wool, often 40—50 mm in size, which drift with the currents and fasten in fishing nets. The tufts or pellets usually consist of stalks only, as the diatom cell easily falls off. Occasional cells do, however, adhere and, in exceptional cases, a large number of cells are found in this material on the nets. The stalks are extremely strong and tough, and when they have wound themselves round the fine threads of the nets they are difficult to remove. If the nets are allowed to dry up completely (Figs. 3 and 4) they are somewhat easier to clean, but if they are seriously clogged it is almost impossible to remove the substance without damaging the nets in some measure. It appears to be quite clear that these gelatinous stalks, which are found in a number of *Diatomaceae*, always consist of pectins, probably of varying consistency and water content. I have found them extremely resistant to rot and decomposition. A sample of these tufts of *Didymosphenia*, kept in a large glass jar of ordinary lake water, showed no sign of decomposing after a year. One must, then, take into consideration the fact that tufts torn loose quite a long time ago can cause difficulties to net fishing. At low water in the rivers and during calm periods in the lakes these tufts sink to the bottom. Then, at high water in the rivers and high winds over the lakes, they circulate once again in the currents and fasten on the nets. This is also confirmed by the fact, mentioned above, that the stalks in these tufts on the nets are usually devoid of alga cells.

I have found this Diatom in such quantities as to obstruct fishing in the following Swedish waters:

Akkajaure Lake, at the mouth of the river Vuoljaätno, at the source of the river Luleälven, Lappland.

Lake Fångsjön, below the Ulriksfors Rapids, in the river Faxälven, Jämtland. In the river *Indalsälven*, in the reach Lake Storsjön—Lake Gesundasjön, Jämtland.

Gimå River, in the Ljungan's river system, Medelpad. (Sample received.)

Lake Vänern, mainly in the eastern waters, Västergötland. Plentiful in some years.

Fishermen in Lake Vänern and the rivers, Indalsälven and Faxälven, have believed this clogging of nets to be caused by waste products from pulp mills. When dry on the nets the material does in fact macroscopically resemble the pollution caused by tufts of wood fibres. When wet, however, it is more like bunches of fungi — *Leptomitus* in particular. This diatom must, however, be regarded as a pronounced pure water form occurring in, for instance, mountain waters. In these waters it can be obstructive to net fishing above

industrial works. In the Faxälven at the rapids, Ulriksfors, it grew on rocks in the rapids above the point at which the waste water from what was at that time a sulphite pulp mill entered the river.

In the literature we find the following mention of *Didymosphenia geminata* in Sweden:

Lule Lappmark, CLEVE (1895). *The Sarek Area*, HUSTEDT (1924), »im ganzen Gebiet verbreitet und nicht selten». Very common on dripping rocks in the lake at Snadvavagge and in the stream Säkojokk. *Abisko Area*, HUSTEDT (1942). In the Abiskojokk among others. Northern Jämtland, FONTELL (1917). In the Åleälv at the falls at Tegefors. The falls, Ristafallet, Lake Ö. Norn, on rocks. The stream Niagara, Storlien — »Massenhaft oder häufig in den meisten Proben». Lake Landösjön, the Långan river system — fairly common, according to N. QUENNERSTEDT. All the sites listed above lie in the mountainous region of Northern Lapland and Jämtland, in both running water and lakes. On the other hand, the sites I, myself, have mentioned in the rivers Faxälven, Indalsälven and Ljungan are situated below the mountains. In these cases the typical sites are rocks washed by the water in steep rapids.

The most interesting point, however, is the fact that the species is found so far south as the great lakes Vättern and Vänern. STÅLBERG (1939), reported it in Lake Vättern. He found it in large quantities just below the water line on exposed rocks along the shores. »The lower part of the *Ulothrix zonate* zone is often white — tinged by the mucilage stems of *Gomphonema geminata*.» In Lake Vänern it was observed by VALLIN (1940). In some years it is found in plenty and its most important sites are those on the surf line of rocks out in the open lake.

As regards its occurrence in other countries, I would like to point out briefly that numerous sites have been reported in Finland, particularly in the northern areas, BACKMAN and CLEVE-EULER (1922), CLEVE (1895). In Central Europe this species of *Diatomaceae* must be regarded as a rarity. It appears to occur only in Switzerland, in Lake Geneva and St. Bernhard lakes (MEISTER 1912), and in England and Scotland (SMITH 1853): not uncommon in subalpine streams. According to WEST: »Often forming felt-like masses of greyish-white colour on dripping rocks.»

Summary

The Diatom, *Didymosphenia geminata*, is relatively common in certain mountainous regions of Northern Sweden, both in streams and lakes. It has also been found in some Norrland rivers below the mountains, where it grows in the swiftest rapids. Further, it is common in the two large lakes of Southern Sweden, Lake Vättern and Lake Vänern, where it is found on exposed rocks on the shores of the lakes and on the surf lines of rocks out in open waters.

In a number of lakes situated below falls and rapids in these Norrland rivers, and particularly in Lake Vänern, this Diatom grows in such profusion that it has temporarily obstructed fishing — the drifting tufts of the stalks fastening in the gill nets.

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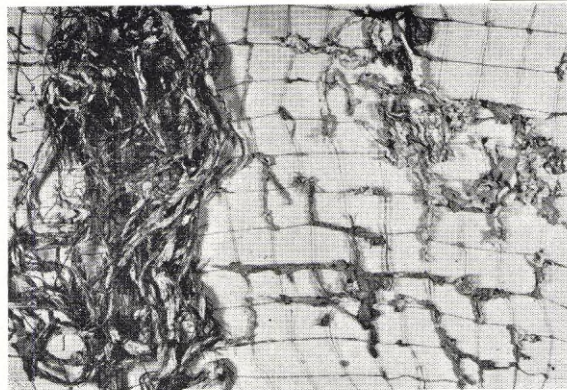
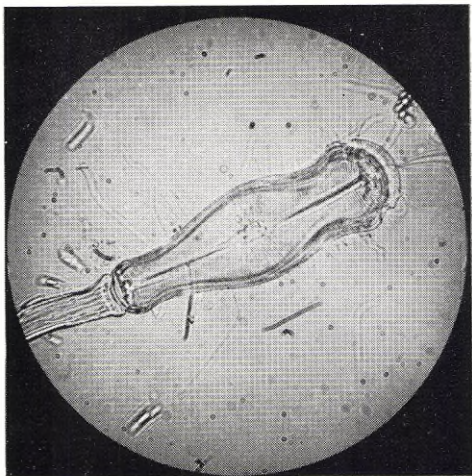
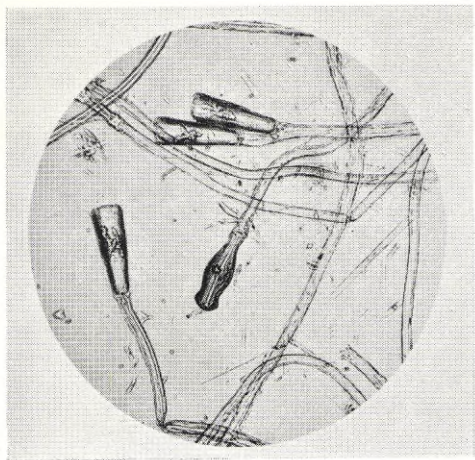


Fig. 1 (above left). *Didymosphenia gemminata* 70 \times .

Fig. 2 (above right). *Didymosphenia gemminata*. 315 \times .

Fig. 3 (left). Net with dry tufts of *Didymosphenia*. $\frac{1}{6}$ \times .

Fig. 4 a—b (below). Dry tufts of the alga with cells taken from the gill nets. 14 \times .



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