GÖTEBORGS UNIVERSITET

ANNUAL REPORT

FOR THE YEAR 1954

AND

SHORT PAPERS

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Director's Report for the Year 1954

By Sven Runnström

Members of the Staff in January 1955

Director:	SVEN RUNNSTRÖM, fil. dr.
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	ERIC FABRICIUS, fil. dr.
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	BARBRO JÖNHED
	GUNNEL NORDEBÄCK
Porter:	ALGOT SJÖLANDER
Kälarne Research Station (in the Province of Jämtland)	
Fishery Assistant:	ELOF HALVARSSON

NILS-ARVID NILSSON has been employed as an extra fishery biologist and ANDERS TÄGTSTRÖM as an extra laboratory assistant. The Porter, Mr. JOHANSON, was ill during the whole year and was replaced by Mr. SJÖLANDER.

The chairman of the Migratory Fish Committee, fil. dr. GUNNAR ALM, and the laboratory assistant of the Committee, ANNA AHLMÉR, had their office at the Institute.

Dr. KARL MÜLLER has worked temporarily at the Institute during a part of the year.

Scientific and Practical Work by the Staff

BRUNDIN, who resumed his duties in June at the conclusion of his expedition to Chile and Peru, has been engaged in working up material of bottom fauna collected earlier from arctic lakes.

NILS-ARVID NILSSON has concluded his investigation of the nutritional biology of the brown trout and the char and the results are published as a special paper in this volume.

LINDSTRÖM has been making an examination of the relations between fish and crustacean plankton, which primarily included the char's and whitefish's choice of food from the plankton of the lake. The char observations have been concentrated to Lake Ottsjön, where LINDSTRÖM previously carried out quantitative plankton investigations. The whitefish observations took place in the Arjeplog district and a similar choice of nourishment was established for the fry of all the three species of whitefish occurring there. These studies of the relationship between fish and plankton are aimed at obtaining increased knowledge if possible of the mechanism, which causes the size of the year classes of the fish to show such a marked variation from year to year.

SVÄRDSON's collecting of whitefish material has continued during 1954. As was the case during the previous year, the heads have been collected for the most part, together with scale samples and particulars of length etc. An extremely large amount of material has been collected, especially as all the fishery assistants, who carry out investigations in regulated lakes, at the same time collected samples of the whitefish they caught. A special expedition was made during the autumn of 1954 to the large lake of the River Klarälven, Lake Femunden in Norway, from which a large (560 specimens) and extremely interesting collection was brought back, as was also the case from some lakes in Southern Sweden.

Working up has been carried on continuously during the year and Mr. TÄGTSTRÖM, the whitefish assistant specially engaged, could count the gillrakers on a very large number of preserved whitefish heads.

Altogether during the year about 8,000 whitefish have been examined, bringing the collected material up to about 20,000 specimens, distributed over the entire Scandinavian Peninsula as well as the Baltic. Certain rivers with many lakes are of such great importance for the solution of the whitefish problem that large quantities of whitefish have been collected from them,

as for example more than 3,000 whitefish from the Ångermanälven river system.

It is now clear that the main variation of the whitefish is the result of the immigration of several different species one after another. The successive emigrants penetrated to different distances up the lakes of the rivers. There has also been a subsequent intensive hybridization. The whitefish constitute, in other words, an example of the role, which introgressive hybridization can play in the evolution of fish. In recent years this evolution mechanism, which was previously considered as being more specially botanical, has been given an ever increasing role in the animal kingdom, as new cases were discovered. In Pisces it seems to be of special importance, as has already been partly established by the pioneer work carried out by HUBBS showing that hybridization between fish is relatively common in nature.

The immigration of the whitefish in the river system of the Scandinavian peninsula and subsequent isolation in different basins opens up unprecedented possibilities for studies of the ecological mechanism of species formation, especially as regards competition between different species for similar food and habitats. Generally speaking it can be said that the large deep lakes, which offer more ecological niches and greater possibilities for decreased competition over food resources, have more sympatric populations than the smaller, shallower lakes. The length of time isolation has lasted is also in certain cases known to a fair degree, as the post-glacial geology of Sweden has been rather thoroughly investigated. It is regrettable from a theoretical viewpoint, however, that many transplantations have been made during the last few hundred years. In this way an abstruse factor has been introduced into the field. The opinion has been advanced to the administrative authorities that transplantation should be forbidden in certain stated lakes in future, so that they could be reserved for future investigation. An additional reason is that the transplantations are undoubtedly more or less worthless from an economic point of view.

With regard to the *pike,* the regional investigation has been continued during the year with the collection of 5,853 scale samples of pike from experimental waters. Altogether detailed particulars of length, weight, sex, date of capture, tackle and scales are now available for 46,244 pike and in addition for approximately 2,000, which were caught in test fishing carried out by the Institute at Drottningholm and in Lake Halmsjön.

Scale-reading of this copious material has not yet been commenced. The difficulties in interpretation mentioned in the report for last year remain unsolved. The collection of control scales from fin-clipped pike of known age continues, mainly now from Lake Öjesjön in Dalarna, and altogether the number of such samples has now reached approximately 60. It is still difficult to reconcile their known age with the checks marked on the scales,

which indicate more periods of arrested development than the winter periods known to have been experienced.

It is possible that the first plan decided upon, what was assessment of age of the pike and direct observations as to whether the year classes reinforced with transplantation really became larger, must be abandoned. But it is probably still possible to observe to a certain extent if the transplantation of fry, which was carried out in the experimental waters, entailed an increase in captures of such an extent that it does not depend on a change in the intensity of fishing or on chance.

The definite working up of this material will not be able to be started until after the material for 1955 has also been received, that is to say at the New Year in 1956 at the earliest. The year 1955 is the last year material is to be collected for the investigation, which will then have covered a period of ten seasons, namely 1946—1955, in accordance with the plans agreed on at the beginning of the experiment.

ALM has in the main concluded during the course of the year his experiments on artificial hybridization between different species of the salmon family carried out at different hatcheries and at the Kälarne Fishery Research Station in particular. Salmon, sea trout, brown trout, f. *lacustris* and f. *fario*, char and brook trout have been included in the experiments. More than 80 such experiments have been made all told. The aim of the experiments was to learn the mortality in the crosses, especially in the eggs and alevin stages and the rate of growth, appearance, sexual maturity and fertility in the grown-up hybrids. Many hybrids were also kept alive and returned to the ponds at Kälarne for genetical and ethological studies by specialists. ALM has written in this report a paper about some of the results obtained. Thus it was established that possibilities for hybridization existed between the species of fish mentioned except between salmon and char and salmon and brook trout. Yet the mortality varied a lot in the different crossings. It was lowest in the char×brook trout crosses, a little higher in the salmon×sea trout crosses, still higher in the salmon×brown trout crosses and highest in the trout×char and trout×brook trout crosses. The extent of the mortality thus confirmed the closer or remoter relationship of the species in question, such as it is generally accepted by the systematists. The same thing is the case regarding sexual maturity and fertility in the hybrids. The char×brook trout hybrids have all been fertile, yet the males in one experiment were difficult to strip. It was possible to get an F2 generation and the backcross also succeeded at least with the brook trout. The salmon, sea trout and salmon×brown trout hybrids have also become sexually matured, but the F2 and backcross experiments have only given very poor results. Only a few eggs have hatched, and the alevins soon died. The trout×char and trout×

brook trout hybrids have not been fertile, but some of them had gonads with small eggs and milt.

The rate of growth has generally been rather good. The colour and appearance have varied a lot, some characteristics of the hybrids being intermediary, others being as one of the parents. Only the trout×char and trout×brook trout hybrids had an appearance very unlike the parents, but rather the same in both these crossings, the sides of the fish having a pattern of pale vermiculation on a dark ground. The char×brook trout hybrids have been rather resistant to high water temperatures. They ought to be produced on a larger scale for stocking of small lakes.

ALM's experiments on the connection between growth and sexual maturity have been continued at the Kälarne Fishery Research Station. They have further confirmed the earlier preliminary results (ALM, Annual Report for the Year 1953). It is thus evident that it is the specimens displaying the best growth in a population (raised in a pond), that first attain sexual maturity. And these specimens generally continue with their good growth, in spite of earlier sexual maturity and despite repeated, often annual, spawning. In populations with different growth rates, for the above-mentioned reasons, the number of spawning specimens at a certain age is greater, when the growth of the population has been good, and lower when the reverse has been the case. This has now been established from a large number of experiments with brown trout f. *lacustris,* brown trout f. *fario,* brook trout, grayling, perch and roach. ALM will present the results of these experiments in a future report from the Institute.

During the year observations on different populations of fish such as whitefish (SVÄRDSON), brown trout (GUSTAFSON, RUNNSTRÖM), grayling (GUSTAFSON) and char (RUNNSTRÖM) has continued. The observations have now extended over a series of years and special attention has been devoted to what might be called meteorological influence on fishery biology, that is to say the temperature conditions of the different calendar years and their influence on the populations of fish. This concerns the wider zones of growth on the fish scales in the warm years and the proportionate strength of the year classes in relation to the excess heat of the year in question. SVÄRDSON has also studied the effect of climate on the large fluctuations in the salmon populations by means of hard winters in the Baltic. With regard to the latter question, which has been to the fore for many years, further data has been collected during the course of the year from different quarters, which may be seen in greater detail in a special paper in this report.

In connection with observations on fish populations marking experiments have been done. The following table gives a survey of the markings carried during 1954 as well as the recaptures from markings during this and earlier years received by the Institute and registered during this year.

Species	Number of fish marked	Number of recoveries
Salmon	36,337	1902
Sea trout	2,115	195
Salmon×Sea trout	136	47
Sea trout×Salmon	318	47
Trout	643	125
Char	976	228
Grayling	401	37
Whitefish	582	139
Pike	190	80

FABRICIUS has continued his studies on the spawning behaviour in some species of fish.

Six females and one male survived of the char that spawned in our tanks in September 1953, while the others were killed by Saprolegnia (see Rept. 35, p. 58 ff.). The survivors changed to the silvery non-reproductive colours in the months of early spring. In July a dark strip appeared on the flank of 3 of the females, and this was the first sign of a gradual change to the spawning markings.

In the middle of August the cooling system of the tank was switched on, and the water was cooled down to the normal spawning temperature. The male and three of the females retained their silvery colour, but in the three ripening females the spawning colouration was gradually completed. Their aggressiveness increased, and they began to show courting activities as well. In the beginning of September they showed a clear migratory behaviour, swimming to and fro in the tank, and they began to be interested in a gravel bottom that had been arranged at one end of the tank. In the middle of September these three females spawned, two of them with a male hybrid between brook trout and char, and the third with a new male char, which was introduced later on. The nest-digging began on September 12th, and the first spawning was observed on September 14th. The spawning run in the River Blåsjöälven, from which these char originated, did not begin until about September 22nd. One of the females guarded its nests for about 10 days after spawning, which is a much longer time than we had observed in our earlier experiments. The young hatched and they seem to grow very well in our tanks.

These experiments show that it is possible to keep char in aquaria for years, following their annual cycle of life, and that the factors influencing migratory behaviour and spawning in salmonids can be studied experimentally under laboratory conditions.

Comparative studies were started on the spawning behaviour of the brook trout, the brown trout, the atlantic salmon and some hybrids between these species. Some interesting differences in their behaviour were found.

In February the spawning behaviour of the burbot was studied in aquarium

tanks. Preliminary studies on the spawning behaviour of the grayling were started in April and May, using the stream water tank of the Hölle laboratory.

Experiment with Tackle

During the year 1954 the employment of twined nylon nets for freshwater fishing has become general and in commercial fishery nylon yarn of this type is almost universally used. There is no doubt that the economic results of the fishing industry have increased very considerably through the greater yield per net and the increased durability of the nets.

MOLIN is continuing the experiments, begun many years ago, on the suitability of different types of nylon for various sorts of tackle. Recent experiments in particular have been aimed at comparing the fishing capacity of the twined nylon yarn and the monofilament nylon. In earlier experiments the superior fishing qualities of the monofilament nylon yarn have been established, being on an average approximately 7 times as great as cotton yarn, and the reliability of these figures has been confirmed by repeated experiments. The experimental nets in all this test fishing have been of the shallow type, roughly speaking approximately 1.5 metres deep. In the 1954 experiments, therefore, nets with a depth of 3.60 m—6.60 m were included. These results were quite surprising and it appeared that the extra yield of captures with the monofilament yarn compared with the twined nylon became less the deeper the net was. Nets of monofilament yarn 3 metres deep gave approximately double as big catches as the same sized nets of twined yarn, while the catch with nets 6 metres deep yielded identical captures or inconsiderably greater ones. Experiments have also been made in manufacture and test fishing with salmon nets, 6 metres deep, made of 0.45 mm monofilament nylon, size 150 mm. stretched mesh. The strength of the yarn proved, however, to be too weak for the purpose, so the dimension should be raised in future experiments to 0.50 mm.

In lakes with very muddy water the fishing capacity of the monofilament yarn falls, as has been previously demonstrated, in proportion to the degree to which it becomes muddied, and this is especially the case when the nets are lying exposed during a long continuous period of time. This disadvantage has, amongst other things, been particularly apparent in certain parts of Lakes Vänern and Hjälmaren.

Publications in the Year 1954

Rep. = *Report from this Institute.*
SFT = Svensk Fiskeritidskrift (Swedish Fishery Journal). Only Swedish language.
ALM, G. Maturity, mortality and growth of perch, *Perca fluviatilis* L. grown in ponds. Rep. 35: 11—20.

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— Laxfisket och laxbeståndet i Östersjöområdet under senare år. *Sv. Vattenkraftförening 441: 41—100.*

— »Tusenbröderabborrarnas» ålder och livslängd. *SFT 63: 134—136.*

— Laxfisket och smålaxfångsten i Östersjön. *Ostkusten 26: 18—21.*

BADCOCK, R. M. Studies of the benthic fauna in tributaries of the Kävlinge river, southern Sweden. *Rep. 35: 21—37.*

— Comparative studies on the populations of streams. *Rep. 35: 38—50.*

BERG, S. Förhållandet mellan laxfångsterna i havet och i älvarna. *SFT 63: 38—40.*

— Redogörelse för fiskeförsök i Bondsjön och Häggsjön. 1951. *SFT 63: 40—43.*

FABRICIUS, E. Aquarium observations on the spawning behaviour of the burbot, *Lota vulgaris* L. *Rep. 35: 51—57.*

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— Beteendeforskning i akvariet. *Akvariet 28: 1—10.*

FABRICIUS, E. and BOYD, H. Experiments on the following-reaction of ducklings. *Rep. Wildfowl Trust Slimbridge 6: 84—89.*

FABRICIUS, E. and GUSTAFSON, K.-J. Further aquarium observations on the spawning behaviour of the char, *Salmo alpinus* L. *Rep. 35: 58—104.*

— Rödingens lekbeteende. *SFT. 63: 86—89.*

FABRICIUS, E. and LINDROTH, A. Experimental observations on the spawning of whitefish, *Coregonus lavaretus* L., in the stream aquarium of the Hölle laboratory at River Indalsälven. *Rep. 35: 105—112.*

LINDROTH, A. A stream tank at the Hölle laboratory. *Rep 35: 113—119.*

LINDSTRÖM, TH. Non-reproductive migrations in the char, *Salmo alpinus* L. *Rep. 35: 118 —132.*

— Om fiskbestånd och fiskets lönsamhet. *SFT 63: 3—8.*

MOLIN, G. Ultraviolett strålnings inverkan på bomulls- och nylongarn. *SFT 63: 26—28.*

MÜLLER, K. Investigations on the organic drift in north Swedish streams. *Rep. 35: 133—147.*

— Produktionsbiologische Untersuchungen in Nordschwedischen Fliessgewässern. Teil: 2. Untersuchungen über Verbreitung, Wachstum und Ernährung der Fische der Nordschwedischen Waldregion. *Rep. 35: 149—183.*

— Flottledsrensningars inverkan på fisket. *Sv. Flottledsförbundet 28: 5195—5205.*

— Fiskeribiologiska undersökningar i vinterdämda sjöar. *Sv. Flottledsförbundet 28: 5206—5210.*

— Fiskeribiologiska undersökningar i olika svenska flottleder. *SFT 63: 22—26.*

— Untersuchung über den Einfluss der Flösserei auf die Fischbestand und die Fischnahrung. *Finlands Flottarförenings årsbok XXII: 34—85.*

NORDIN, S. Ökade fångster genom förbättring av noten. *SFT 63: 150—151.*

RUNNSTRÖM, S. Director's report for the year 1953. *Rep. 35: 5—10.*

SCHMUUL, R. Är gösfiskeförbud under lektiden berättigat. *SFT 63: 58.*

STENDAHL, B. Skadeverkningar på fisket genom avloppsförorening. *Lantbrukstekniska kalendern 1954: 143—148.*

— Något om vattenförorening och möjligheterna att motverka densamma. *Hygienisk Revy nr 3, 1954: 115—134.*

— Vattenvård hemma och ute. *SFT 63: 75—76.*

STJERNA-POOTH, I. Über das Einwirken des Grubenwassers auf die Kieselalgenflora in einigen oligotrophen Seen in Västerbotten. *Rep. 35: 184-209.*

SVÄRDSON, G., Stora fiskbestånd eller bestånd av stora fiskar. *SFT 63: 54—57.*

SÖRENSEN, I. *Gonyostomum semen* (EHRENB.) DIESING — en vattenorganism av teoretiskt och praktiskt intresse. *Sv. Faunistisk Revy 2: 47—52.*

— Blomkålssjuka hos ål. *SFT: 96—97.*

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Artificial Hybridization between different Species
of the Salmon Family

By GUNNAR ALM

Contents

I. Introduction

In nature interspecific and at times even intergeneric hybrids between closely related species of fish are not infrequently encountered. This is particularly the case among the Cyprinidae and the Sunfishes (KNAUTHE 1896, GEYER 1937, HUBBS 1932, 1943 and others). Possibly hybrids also occur in other groups of fish, although the progeny are then similar to one of the parents and are therefore generally unrecognizable as hybrids. Thus the origin of such hybrids often becomes uncertain.

Even in the earlier stages of fish-culture artificial hybrids were produced, however, especially between different species of the Salmon family. This was particularly the case in England (DAY 1884, 1887) and Germany (HOFER 1909 etc.). Such artificial hybrids have also been produced more recently.

(FOERSTER 1935, JONES 1947, WINGE and DITLEVSEN 1948, STOKELL 1949, STENTON 1952).

Such experiments with artificial hybridization are of great interest. Hybrids and especially their sexual products, to the extent that such are formed, are a valuable subject for genetic studies on questions of species and family. It is also of interest with regard to specification problems to know what the possibilities are for hybridization between different species. Furthermore it is of importance to make clear, in which cases a hybridization achieved by artificial means is so easy, that it gives reason to suppose that such hybridizations often occur in nature, provided that the prerequisites exist. For ethologists it is interesting to study the behaviour of the hybrids as compared with that of the parents. It is also possible that some valuable characteristic of one of the parents can be combined with some other such characteristic in the other. In addition a study of the growth and fertility of the hybrids is of general interest. Provided that they have a better capacity for growth than the parents, it can be of value to produce such hybrids for transplantation. They can also be tested in competitive experiments with the parents. In the cases where the hybrids can be definitely distinguished from the parents, and on the assumption that they are just as viable, the transplantation of hybrids into waters, where both the parents are to be found, can be a means of testing the value of fishculture.

Artificial hybridization between different species of the Salmon family was included in the program of work at the Kälarne Fishery Research Station for the above-mentioned reasons. The purpose of the experiments has been twofold. It has partly been a question of testing the possibility of hybridization between different species as well as studying the mortality, rate of growth and fertility of the hybrids obtained as compared with the parents. The experiments have also been partly aimed at obtaining a large amount of material both preserved and living for future use in systematic and genetic studies as well as for observations on behaviour. In the present paper only the first-mentioned points have been touched upon broadly speaking. It has also been considered suitable in this connection to provide a summarized survey of the available literature dealing with artificial hybridization, especially where the Salmon family is concerned.

II. Material and Methods

The species of fish, which have been included in the hybridization experiments carried out in this way, have been Salmon (*Salmo salar* L) =S, Sea trout (*Salmo trutta trutta* L) =St, Brown trout (*Salmo trutta*) =Bt, including the forms *lacustris* L=Btl and *fario* L=Btf, Char (*Salmo alpinus* L) =Ch, and Brook trout or Speckled trout (*Salmo fontinalis* MITCHILL) =Bkt.

Collection of spawn and fertilization as well as hatching have been carried out at the hatcheries at Mörrum (River Mörrumsån in Southern Sweden), Borenshult (Lake Vättern), Älvkarleby (River Dalälven), Kvarnbäcken (River Indalsälven) and at the Kälarne Research Station in the Province of Jämtland.

As the aim was to obtain an idea of the average losses with these crossings, to avoid the influence of accidental factors, which perhaps would have a positive influence in one hatching season, and a negative influence in another, several experiments with the same species were usually made, The experiments have therefore been carried out during entirely different years, depending on the availability of the desired breeding fish. Strict control experiments have usually been made, particularly in experiments with salmon ×sea trout. The spawn from a female fish has been divided into two parts, one of which was fertilized with milt from the species one wished to cross and the other with milt from the same species as the female fish. In the male fish the same male was thus used for both pure bred and cross fertilization.

For the purpose of obtaining if possible an idea of the mortality during different periods of the development of the ova, a division has been made into three periods, namely: 1) the period from fertilization to the eyed ova stage 2) the time from this to the hatching stage itself and 3) the time until the absorbtion of the yolk sac, that is to say the transplantation stage. Unfortunately the notes, which were made at the different hatcheries, were often quite brief and in certain cases did not permit any reliable division of the mortality into different periods. In all experiments and in references in the text the female is placed first.

The continued rearing of the fry has most often occurred during the first summer at Kvarnbäcken in small wooden troughs and later at Kälarne in the ponds belonging to the Research Station. The troughs at Kvarnbäcken were $3 \times 0.8 \times 0.4$ m in size with a water flow of 15—25 l/min. The temperature of the water seldom exceeds 15 to 16° C and the pH value is 7.5. The ponds at Kälarne are approx. 85×8 m and approx. 0.8 m deep with a water flow of approx. 250 l/min. The water is clear with a pH value of approx. 7.0 and a maximum temperature of 22 to 23° C.

In the troughs each species or hybrid has as a rule been kept separate. The fry from the hybrids as well as from the parent fish have in some cases, however, been reared in the same trough. The number of fry introduced has varied between 500 and 2000 in every trough, that is to say approximately 200—800/m². In all these experiments with rearing of fry in troughs ample food has been provided during the entire summer. The varied density of population, which has partly been caused by the different numbers of the fry introduced, partly by dissimilar mortality in the different experiments, has regarding to previous experiments with salmon (ALM 1938), only had a very little influence upon the growth.

A number of the one-summer-old hybrids have been transplanted into

lakes or preserved, others have been introduced into ponds. Most frequently when reared in ponds several species of fish have been kept together. Attempts have also been made to try to keep about the same number of fish of the same size in every pond. A good supply of natural food occurred in the ponds, and in addition feeding with coarsely ground or chopped fish has taken place.

These experiments could not have been carried out and the necessary material for them obtained without the help of the superintendents at the above-mentioned hatcheries and at the Kälarne Fishery Research Station. To all these persons, and especially to G. Molin, A. Andersson and E. Halvarsson, I should like to give my heartiest thanks for their very valuable assistance.

III. **Results**

1. *Mortality.*

E g g s   a n d   a l e v i n s   b e f o r e   l i b e r a t i o n   o f   t h e   f r y.

In Table 1 a survey is given of all the hybridization experiments and the results up to the stage of the absorbtion of the yolk sac and the liberation of the fry.

Salmon, Sea trout and Brown trout f. f a r i o. The most comprehensive experiments have been concerned with Salmon and Sea trout. When two experiments were made in the same year at a certain hatchery the female fish in one of the experiments was a larger specimen, than in the other experiment. Mortality has varied considerably in these experiments, as was the case in all the rest. Regarding the Salmon × Sea trout [1] hybrids (Table 1 exp. 1—15) 53,450 fry were obtained from a total of 75,970 eggs put in, which represents a mortality of nearly 30 %. From Sea trout × Salmon (exp. 16—28) the 52,460 eggs obtained gave 29,730 fry, that is to say a mortality of about 43 %. Thus the mortality has been greater in the eggs from Sea trout × Salmon than in the reverse crossing.

In Table 2 the mortality figures have been grouped together for all the series of experiments with salmon, where control experiments took place at the same time. Mortality has been greater in all the hybridization experiments with Salmon × Sea trout than in the control experiments, in several cases much greater. In some cases the hybridization experiments have yielded entirely negative results. Greater mortality has usually been found in the experiments with Sea trout × Salmon hybrids, but the control experiments have often been poor as well with losses amounting to as much as 85 % and in one experiment 100 %. The reasons for this are discussed later (page 44).

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[1] The female species is always mentioned first.

Table 1. Review of the hybridization experiments.

Experiment	Parent fish (the females always first)	Hatchery	Hatching season	Number of eggs in the experiment	Number of dead eggs and fry in the periods				Number of fry for liberation	Losses in % of number of eggs
					spawntaking to eyes visible	eyes visible to hatching	hatch, to absorb of the yolk sac	total		
1	2	3	4	5	6	7	8	9	10	11
1		Kv.[1]	1935/36	6,000	800	125	205	1,130	4,870	19
2		M.	1948/49	8,500	40	460	300	800	7,700	9
3		»	»	3,800	90	590	720	1,400	2,400	37
4		Ä.	»	6,300	900	800	2,800	4,500	1,800	71
5		»	»	1,560	10	810	40	860	700	55
6		Kv.	»	3,100	1,700	1,090	310	3,100	0	100
7		»	»	1,200	60	240	900	1,200	0	100
8	S × St	M.	1949/50	5,760	130	470	200	800	4,960	14
9		»	»	4,200	210	850	250	1,310	2,890	31
10		Ä.	»	8,400	30	200	1,130	1,360	7,040	16
11		»	»	4,000	30	140	520	690	3,310	17
12		Kv.	»	4,500	190	230	570	990	3,510	22
13		»	»	2,000	110	440	270	820	1,180	41
14		M.	1951/52	9,300	100	215	625	940	8,360	10
15		Ä.	»	7,350	1,705	555	355	2,165	4.735	64
16		Kv.	1945/46	7,000	400	630	70	1,100	5,900	16
17		»	1946/47	5,000	2,010	400	1,590	4,000	1,000	80
18		M.	1948/49	4,200	30	470	20	520	3,680	12
19		»	»	2,400	50	720	960	1,730	670	72
20		Ä.	»	3,300	760	310	2.290	3,360	0	100
21		»	»	1,200	460	70	320	850	350	71
22	St × S	Kv.	»	1,000	20	160	20	200	800	20
23		M.	1949/50	5,760	10	2,030	310	2,350	3,410	41
24		»	»	3,480	20	500	80	600	2,880	17
25		Ä.	»	4,000	110	310	400	820	3,180	21
26		»	»	2,300	150	890	80	1,120	1,180	48
27		M.	1951/52	5,425	6	180	256	542	4,883	10
28		Ä.	»	5,400	118	4,309	1,013	5,400	0	100
29		Kv.	1935/36	?	—	—	—	—	150	?
30		»	1938/39	4,000		1,500		1,500	2,500	38
31	S × Bt	Kä.	1946/47	2,000	2,000		—	2,000	0	100
32		»	1948/49	3,000	1,400	540	1,060	3,000	0	100
33		»	»	1,200	40	1,145		1,185	15	99
34	Bt × S	Kv.	1938/39	1,400	210	750	440	1,400	0	100
35		Kä.	1948/49	1,000	200	290	85	575	425	58
36	S × Ch	»	1954/55	2,200	210	1,990	—	2,200	0	100
37	S × Bkt	»	1941/42	6,600	1,510	5,090	—	6,600	0	100
38	Bkt × S	»	»	6,200	6,200	—	—	6,200	0	100
39	(S × St) × (S × St)	»	1939/40	355	355	—	—	355	0	100
40	(S × St) × (St × S)	»	1954/55	4,200	3,020	620	560	4,200	0	100
41	(St × S) × St	»	»	2,000	1,300	700	—	2,000	0	100

[1] Kv. = Kvarnbäcken, M. = Mörrum. Ä. = Älvkarleby, Kä = Kälarna, B. = Borenshult.

Table 1 (continued).

1	2	3	4	5	6	7	8	9	10	11
42		Kä.	1944/45	540	140	380	20	540	0	100
43	(S × Bt) × (S × Bt) ...	»	1945/46	4,000	450	300	3,250	4,000	0	100
44		»	1948/49	300	297			297	3	94
45	S × (S × Bt)	»	1946/47	2,000	2,000			2,000	0	100
46	(S × Bt) × S	»	1944/45	850	740	110	---	850	0	100
47		»	1943/44	1,600	700	285	615	1,600	0	100
48	(S × Bt) × Bt	»	1944/45	230	135	80	15	230	0	100
49		»	1945/46	1,000	430	170	350	950	50	95
50	Bt × (S × Bt)	»	1944/45	1,970	980	985	5	1,970	0	100
51		»	1945/46	1,200	125	475	600	1,200	0	100
52	(S × Bt) × Bkt	»	1945/46	1,500	150	1,350	—	1,500	0	100
53		B. Kä.	1938/39	4,000	975		2,130	3,100	895	78
54	Bt × Ch	»	1951/52	11,000	6,500	1,700	1,000	9,200	1,800	84
55		»	1952/53	9,640	6,870		2,170	9,040	600	94
56		»	1938/39	2,800	725		685	1,410	1,390	50
57		»	1943/44	2,000	620		100	720	1,280	36
58	Ch × Bt	»	1944/45	1,740	55			55	1,690	?
59		»	1951/52	12,000	370	4,700	2,000	7,070	4,930	59
60		»	1952/53	2,930	1,740		690	2,430	500	83
61		Kä.	1938/39	5,000	370	1,800	1,830	4,000	1,000	80
62		»	1942/43	1,070	630		55	685	390	64
63	Bt × Bkt	»	1943/44	4,800	3,500			3,500	1,300	73
64		»	1944/45	5,500	1,500			1,500	4,000	27
65		»	1952/53	3,500	2,070	1,430	—	3,500	0	100
66		»	1953/54	9,400	220	1,880	7,250	9,350	50	99
67		»	1942/43	19,800	17,155		2,465	19,800	0	100
68		»	1942/43	2,400	1,400		1,000	2,400	0	100
69	Bkt × Bt	»	1951/52	2,500	580	520	1,400	2,500	0	100
70		»	1952/53	6,000	6,000	—	—	6,000	0	100
71		»	1953/54	11,500	1,970	6,230	3,300	11,500	0	100
72	Ch × Bkt	»	1944/45	1,950	16	4	30	50	1,900	3?
73		»	1951/52	12,500	1,480	2,020	1,500	5,000	7,500	40
74	Bkt × Ch	»	1951/52	6,000	1,700	1,450	50	3,200	2,800	53
75		»	1948/49	11,000	5,200	4,800	50	10,050	950	91
76		»	1948/49	10,000	5,300	1,650	2,600	9,550	450	95
77	(Ch×Bkt)×(Ch×Bkt)	»	1949/50	10,000	1,500	1,400	5,900	8,800	1,200	88
78		»	1951/52	5,000	1,680	1,320	1,000	4,000	1,000	80
79		»	1953/54	8,000	400	3,400	1,200	5,000	3,000	63
80		»	1948/49	3,000	1,120	580	600	2,300	700	77
81	(Ch × Bkt) × Bkt	»	1949/50	3,000	300		1,000	1,300	1,700	43
82		»	1951/52	6,000	700	300	500	1,500	4,500	25
83	(Ch × Bkt) × Ch	»	1954/55	3,100	1,750	680	70	2,500	600	81
84	[(Ch × Bkt) × Bkt] ×	»	1953/54	15,600	5,400	3,480	1,720	10,600	5,000	68
85	[(Ch × Bkt) × Bkt] ...	»	1954/55	6,500	2,360	1,710	330	4,400	2,100	68
86	Ch × [(Ch × Bkt) × Bkt]	»	1954/55	3,700	330	550	520	1,400	2,300	62
87	[(Ch × Bkt) × Bkt] × Ch	»	1954/55	3,400	2,360	750	290	3,400	0	100

Table 2. Mortality in the hatching season (losses in percentage of number of eggs obtained) in the Salmon × Seatrout hybridization and control experiments.

Hatchery	Hatch. season	$S^1 \times St$	$S^1 \times S$	$S^2 \times St$	$S^2 \times S$	$St^1 \times S$	$St^1 \times St$	$St^2 \times S$	$St^2 \times St$
Mörrum	1948—49	9.1	6.1	36.8	13.2	12.4	24.5	72.1	20.8
»	1949—50	13.9	11.5	31.2	18.4	40.8	51.1	17.3	20.3
»	1951—52	10.1	3.2	—	—	10.0	2.7	—	—
Älvkarleby	1948—49	71.4	24.3	55.1	18.3	100.0	84.8	70.8	80.7
»	1949—50	16.2	3.3	17.2	4.7	20.5	11.1	48.1	10.4
»	1951—52	35.5	20.5	—	—	100.0[3]	100.0[3]	—	—
Kvarnbäcken	1948—49	100.0	61.2	100.0	8.3	10.0	29.0	20.0	76.0
»	1949—50	22.0	6.5	41.0	14.0	—	—	—	—

[1] Big females.   [2] Small females.   [3] The eggs not fertilized.

Mortality in the majority of experiments has been greatest during the second and third periods, that is to say in the eyed ova and alevin stages and especially during the hatching itself. In some experiments it has, however, mainly occurred during the first period. Fertilization has undoubtedly been poor or perhaps not occurred at all in these cases. In the greater number of cases mortality has been greater in eggs from smaller female fish.

Experiments with Salmon × Brown trout (exp. 29—33) and Brown trout × Salmon (exp. 34—35) have yielded considerably worse results than with Salmon × Sea trout and also worse than with pure Brown trout eggs. Experiments with Salmon × Char (exp. 36) and Salmon × Brook trout (exp. 37—38) have been entirely negative.

In those experiments, in which the hybrids have become sexually mature (see page 28), experiments have been made both with backcross with Salmon (exp. 45—46), Sea trout (exp. 41) and Brown trout (exp. 47—51), as well as amongst themselves to obtain a F2 generation (exp. 39, 40, 42—44). All these experiments have proved to be negative or have given extremely poor results, as Table 1 shows. Sometimes mortality has occurred even in the earliest periods, in other experiments on the other hand it has occurred later, so that a part of the eggs has hatched (exp. 44, 49) but mortality in the alevins has been very great. Only in experiment 49 have I succeeded in getting a small number of fry, which, however, soon died.

Brown trout f. l a c u s t r i s and Char. The mortality in the eggs of Brown trout × Char and reverse (exp. 53—60) has throughout been greater than in the Salmon hybrids. It has also been greater, 78—94 %, in the experiments with brown trout as the female fish, as opposed to 50—83 % in the reverse crossings (one exp. uncertain). More detailed data about the different periods when the mortality actually occurred are unfortunately not available in the majority of the experiments.

Table 3. Mortality in the hatching season (losses in percentage of number of eggs obtained) in the Browntrout, Char and Brooktrout hybridization experiments and in the parent fish in the same seasons.

Hatch. season	Bt	Ch	Bkt	Bt × Ch	Ch × Bt	Bt × Bkt	Ch × Bkt	Bkt × Ch	(Ch × Bkt) × (Ch × Bkt)	(Ch × Bkt) × Bkt
1938—39	—	—	—	78	50	80	—	—	—	—
1942—43	40	7	—	—		64	—	—	—	—
1943—44	—	—	—	—	36	73	—	—	—	—
1944—45	14	—	1?	—	3?	27	3?	—	—	—
1948—49	—	—	—	—	—	—	—	—	93	77
1949—50	9	—	27	—	—	—	—	—	88	43
1950—51	25	4	61	—	—	—	—	—	—	—
1951—52	20	45	57	84	59	—	40	53	80	25
1952—53	20	14	75	94	83	100	—	—	—	—
1953—54	18	—	40	—	—	99	—	—	63	—

Brown trout f. f a r i o and Brook trout. In the hybridization experiments with Brown trout and Brook trout the experiments with the latter as the female fish (exp. 67—71) have all given negative results. The reverse crossing on the other hand (exp. 61—66) has resulted in fry in four out of six experiments, even if the mortality has generally been great.

Char and Brook trout. Finally as regards the crossing of Char × Brook trout (exp. 72—74), experiments with both species as the female fish have given relatively good results (one exp. uncertain). The mortality has varied between approx. 40 % and 53 %. In a number of backcross (exp. 80—83) and inter-cross (exp. 75—79) experiments with the F 1 specimens the mortality has been considerably greater, but not in any case total. Crossing of backcross females with backcross males (exp. 84—85) or with Brook trout (exp. 86) has succeeded relatively well. Recrossing of such females with Char (exp. 87) has, on the other hand, been entirely negative. Likewise in a backcross experiment between an F 1 female with a Char (exp. 83) mortality has been high.

In Table 3 are grouped the percentage figures for mortality in the above-mentioned experiments, both in the hybrid-eggs and in some control experiments. Here the mortality in eggs from the Brook trout has often been strikingly high, probably depending on bad breeding fish. It is clear, however, that as was the case in the Salmon hybrid-eggs the above-mentioned hybrid-eggs reveal a greater mortality than the parent eggs.

Mortality in the first summer and subsequently.

The fry obtained from the hybrids have partly been transplanted, partly put in troughs and ponds for rearing and breeding. In Tables 4 and 5 are given figures for the mortality in the first summers. When figures are available at the same time for fry from the parent, regard has only been paid to such experiments, where the number of fish put in has been more

Table 4. Mortality in the first summer (losses in percentage of number of fry) in the Salmon hybrids and parent fish.

Year	S	St	Bt	S × St	St × S	S × Bt	Bt × S
1936	35	48	—	94	—	—	—
	3,500[1]	750		1,500			
1939	18	45	54	—	—	53	—
	4,000	1,900	3,000			2,000	
1946	47	20	—	—	54	—	—
	2,000	5,000			1,500		
1947	28	—	—	—	35	—	—
	8,000				1,000		
1949	8	8	49	47	62	—	25
	16,000	3,700	2,500	3,000	1,850		400
1950	14	22	—	53	50	—	—
	5,500	2,500		1,500	1,500		
1952	7	13	—	36	36	—	—
	15,000	1,200		2,500	2,500		

[1] Number of fry at the beginning of rearing.

Table 5. Mortality in the first summer (losses in percentage of number of fry) in the Browntrout, Char and Brooktrout hybrids and parent fish.

Year	Bt	Ch	Bkt	Bt × Ch	Ch × Bt	Bt × Bkt	Ch × Bkt	Bkt × Ch	Ch × Bkt F 2	(Ch × Bkt) × Bkt
1939	32	11	33	54	15	86[4]	—	—	—	—
	1,000[1]	1,000	1,000	500	500	1,000				
1944	25	8	24	—	67	83	—	—	—	—
	3,000	1,000	1,500		660	1,000				
1944	81[2]	10[2]	—	—	26[2]	—	—	—	—	—
	330	330			330					
1944	38[2]	—	64[2 3]	—	—	64[2 3]	—	—	—	—
	330		330			330				
1945	72	—	64	—	—	96[4]	65	—	—	—
	2,300		1,000			1,000	1,000			
1945[5]	81[2]	49[2]	—	—	64[2]	—	—	—	—	—
	500	500			500					
1945	97[2]	42[2 3]	—	—	42[2 3]	—	—	—	—	—
	500	500			500					
1949	48	—	60	—	—	—	—	—	79	43
	2,500		2,000						1,400	700
1950	—	16	—	—	—	—	—	—	54	25
		1,500							1,000	1,700
1952	47	26	—	34	42	—	22	23	—	—
	1,000	1,000		1,000	1,000		1,000	1,000		
1952	—	32[2]	13[2]	—	—	—	—	10[2]	—	—
		300	300					300		
1954	54[4]	—	—	—	—	—	—	—	56	—
	2,400								2,500	

[1] Number of fry at the beginning of rearing.   [2] The three species in the same trough.
[3] The two species not separated.   [4] Reared in ponds.   [5] From Svärdson (1949).

Table 6. Mean length in cm (mean total length) in one-summer-old Salmon hybrids and parent fish.

Year	S	St	S × St	St × S	Bt	S × Bt
1936	4.5	5.9	7.0	—	—	—
	2,300[1]	400	84			
1939	5.6[2]	—	—	—	5.6[2]	5.9[2]
1946	4.3	4.8	—	4.6	—	—
	1,060	3,900		700		
1947	4.6	—	—	4.9	—	—
	5,700			650		
1949	4.5	5.7	4.7	5.3	5.1	—
	1,200	1,180	580	660	1,300	
1950	5.1	6.1	5.3	5.1	—	—
	3,500	1,960	700	750		
1952	—	—	4.5	4.6	—	—
			1,615	1,600		

[1] Number of fish obtained.

[2] In the spring 1940, in the winter 1939—40 in ponds.

or less identical. Where several such experiments have taken place the figures have been added together.

The losses vary very considerably. First as regards the Salmon hybrids a certain tendency towards larger losses in the hybrids is evident. This is especially the case in the later experiments with Salmon × Sea trout hybrids. On the other hand in certain earlier experiments of this kind, mortality has been unusually great in the pure species as well, although even then generally still greater in the hybrids. In the Brown trout × Char and Brown trout × Brook trout hybrids mortality has varied a lot. In certain experiments, where the rearing of the three species took place in the same pond and where competitive conditions played a part, mortality has been considerably higher in the Brown trout, which is evidently inferior in competition. The Char × Brook trout hybrids have also had varying mortality, but on the whole agreeing more with that of the parent fish. Yet in the F 2 generation the mortality has been greater.

2. *Rate of growth, colour and appearance, sexual maturity and fertility.*

The Salmon hybrids. Table 6 shows the mean length (mean total length) of the Salmon hybrids at the end of the first summer, in the majority of cases it also shows that of the fry from the parent fish reared at the same time. In spite of great variations during different years, it appears from these figures that the growth has been better in the Sea trout than in the Salmon, and in the hybrids it has usually been intermediate between those of the parents. Figures 1 and 2 show the variation of the size groups in some of
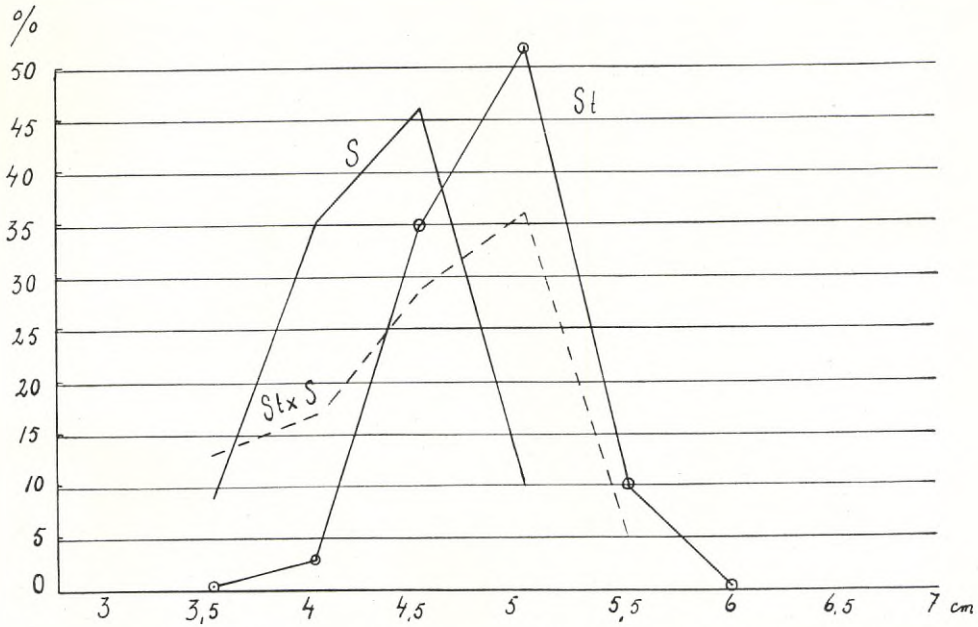
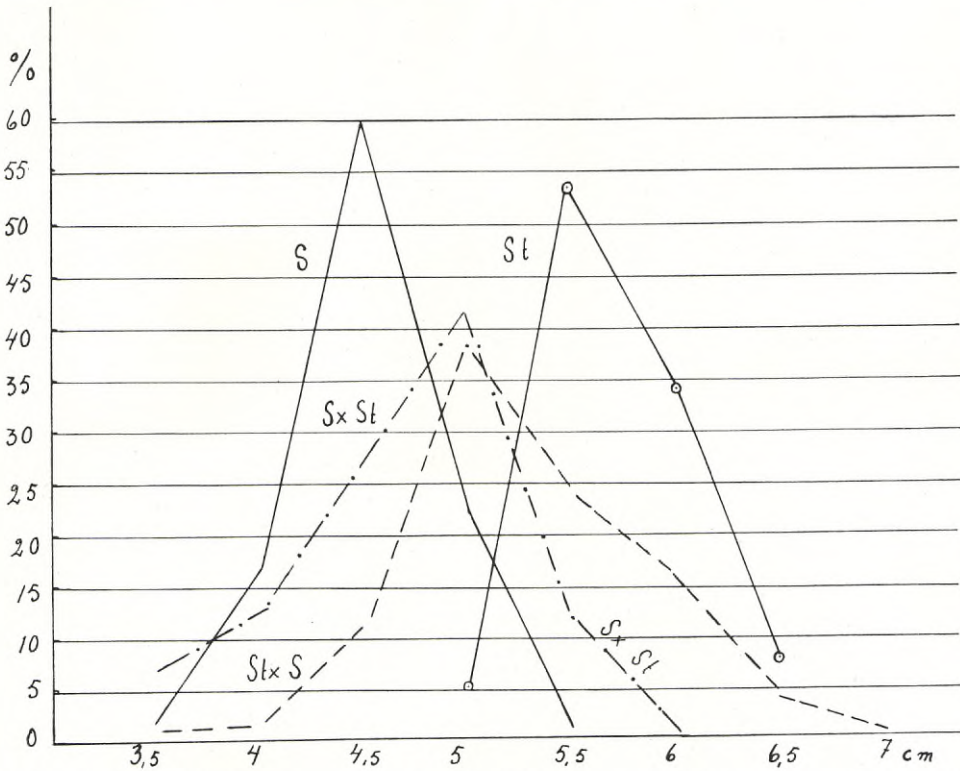Fig. 1. Size distribution of one-summer-old (1946) Salmon, Seatrout and Seatrout×Salmon hybrids.

Fig. 2. Size distribution of one-summer-old (1949) Salmon, Seatrout, Salmon×Seatrout and Seatrout×Salmon hybrids.

Table 7. Salmon hybrids. Number (N) and mean length in cm (Ml) at different ages.

Age in years	S × St						St × S							S × Bt		Bt × S	
	Exp. 1		Exp. 4		Exp. 15		Exp. 16		Exp. 17		Exp. 21		Exp. 27		Exp. 30		Exp. 35	
	N	Ml	N	Ml	N	Ml	N	Ml	N	Ml	N	Ml	N	Ml	N	Ml	N	Ml
1	47	9.6	635	7.3	78	5.1	120	4.7	68	5.4	670	7.3	123	5.3	700	6.5	65	?
2	17	12.8	560	12.6	53	11.1	115	13.5	48	12.4	450	10.0	105	11.4	627	9.7	32	13.3
3	16	24.6	411	16.9	43	18.4	88	20.2	—	—	425	13.0	91	17.2	213	12.5	8	18.0
4	10	28.2	290	24.3	—		50	22.0	—		421	17.6	29	21.3	158	17.8	—	
5	6	34.3	210	32.6	—		48	27.8	—		380	27.6	—		150	19.2	—	
6	5	40.2	45	38.3	—		14	29.0	—		48	34.5	—		54	21.1	—	
7	2	52.5	—		—		8	33.3	—		—		—		26	24.2	—	
8	—		—		—		6	36.7	—		—		—		11	26.8	—	
9	—		—		—		—		—		—		—		10	28.2	—	
10	—		—		—		—		—		—		—		4	29.0	—	
11	—		—		—		—		—		—		—		2	30.8	—	

the experiments. This is greater in the hybrids than in the parents or in every case similar to that of the parents, which shows the greatest variation.

In Table 7 are given figures for number and size in the continued rearing of the Salmon hybrids. Growth varies very much in this rearing, in spite of efforts having been made, to obtain more or less similar conditions through adjustment of the size of the population and feeding. Certain mean lengths for growth are available, however, from a large number of experiments in rearing Salmon in particular but also Sea trout, with which the figures for the hybrids can be compared. In Figure 3 such normal growth-curves for Salmon and Sea trout are given and, in addition, corresponding curves for some of the hybrids. As regards growth in rearing Salmon and Sea trout in ponds, it is always better in the latter species. This agrees as well with the conditions in nature (ALM 1919 and others). The figures as well as Table 7 now show that the growth in the Salmon × Sea trout hybrids is better than or most closely resembles the Sea trout, while the reverse hybrids seem to have a somewhat poorer rate of growth. Mortality has varied but in certain experiments has been relatively high and considerably greater than is normal in rearing Salmon in general. This is also the case for the Salmon × Brown trout hybrids. These have had poorer growth as well.

Concerning the colour and appearance in the Salmon × Sea trout hybrids, mention will only be made here that both hybrids in these experiments, but especially the hybrids Sea trout × Salmon, have had more small spots than Salmon parr, while at the same time the parr marks have been more distinct and more reminiscent of those in the Salmon parr. The shape of the body has often been rather clumsy and with a relatively thick base to the tail, consequently reminding one of the Sea trout. The size of the pectoral fins, on the other hand, has rather been the same as in Salmon. A faintly distinguishable dark edge on certain fins may be attributed to the Sea trout.
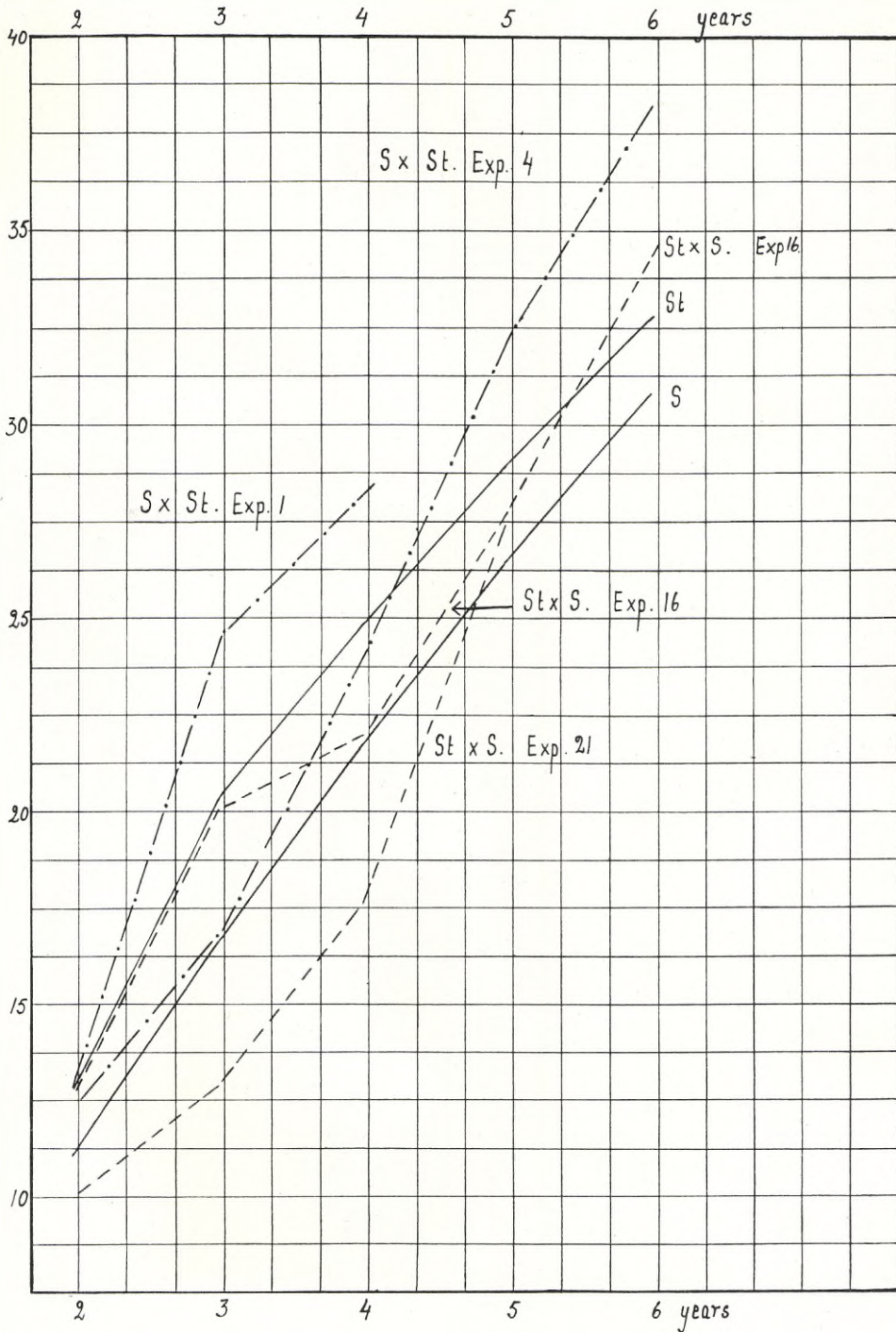
Fig. 3. Rate of growth of Salmon×Seatrout and Seatrout×Salmon hybrids from some of the experiments as well as normal growth-curves for Salmon and Seatrout with rearing in ponds.

Table 8. Salmon hybrids. Number of smolt in percentage of total and mean length (Ml) in cm in smolt and parr.

Age in years		S × St			St × S			S × Bt	Bt × S
		Exp. 1	Exp. 4	Exp. 15	Exp. 16	Exp. 21	Exp. 27	Exp. 30	Exp. 35
2	% Smolt	Most	60.2	0	53.9	13.0	0	10.7	62.5
	Ml. Smolt	12.8	16.6	—	16.8	15.5	—	11.3	15.2
	Ml. parr		11.2	11.1	13.0	10.2	11.4	10.5	11.2
3	% Smolt	68.8	64.9	88.4	Most	?	73.6	10.8	
	Ml. Smolt	22.8	19.0	18.6	20.2	?	17.5	17.0	
	Ml. parr		13.6	17.4	—	—	15.6	12.2	
4	% Smolt	—	81.4	—	—	76.9	—	33.3	
	Ml. Smolt	—	26.0	—	—	18.3	—	18.9	
	Ml. parr	—	16.6	—	—	15.3	—	17.2	

The Salmon×Brown trout hybrids have been still more spotted and mottled red than the Salmon×Sea trout hybrids and have been more reminiscent of Brown trout f. *fario* than of Salmon. The occurrence of black and white edges to the fins was noticeable here, being particularly typical for this trout form (ALM 1939, 1949). The greater number of hybrids have had clear colour marking like this on both the dorsal and anal fins and also, though weaker, on the pelvic fins. This colour marking does not occur, however, on the bright ones, which in other respects more closely resembled Salmon parr, both in colour markings and in shape. The ones with strong colouration of the fins have also had a rather long and narrow body and in this respect have more resembled Salmon than Trout f. *fario*. Colouration of the edges of the fins has still been found in the majority even at an age of 5 to 6 years. At the same time the large parr marks in these hybrids have been very conspicuous remaining clearly discernible even at 6 and in part 7 years of age.

Particulars concerning age and size for the attainment of the smolt stage with the brilliant silvery lustre in the spring, have been grouped in Table 8. Those fish having only a faint silvery colour, but which would undoubtedly have been entirely silvery later, have been included as smolts. As was the

Table 9. Salmon hybrids. Number of sexually mature males (♂) and females (♀) and immature (Im) specimens at different ages.

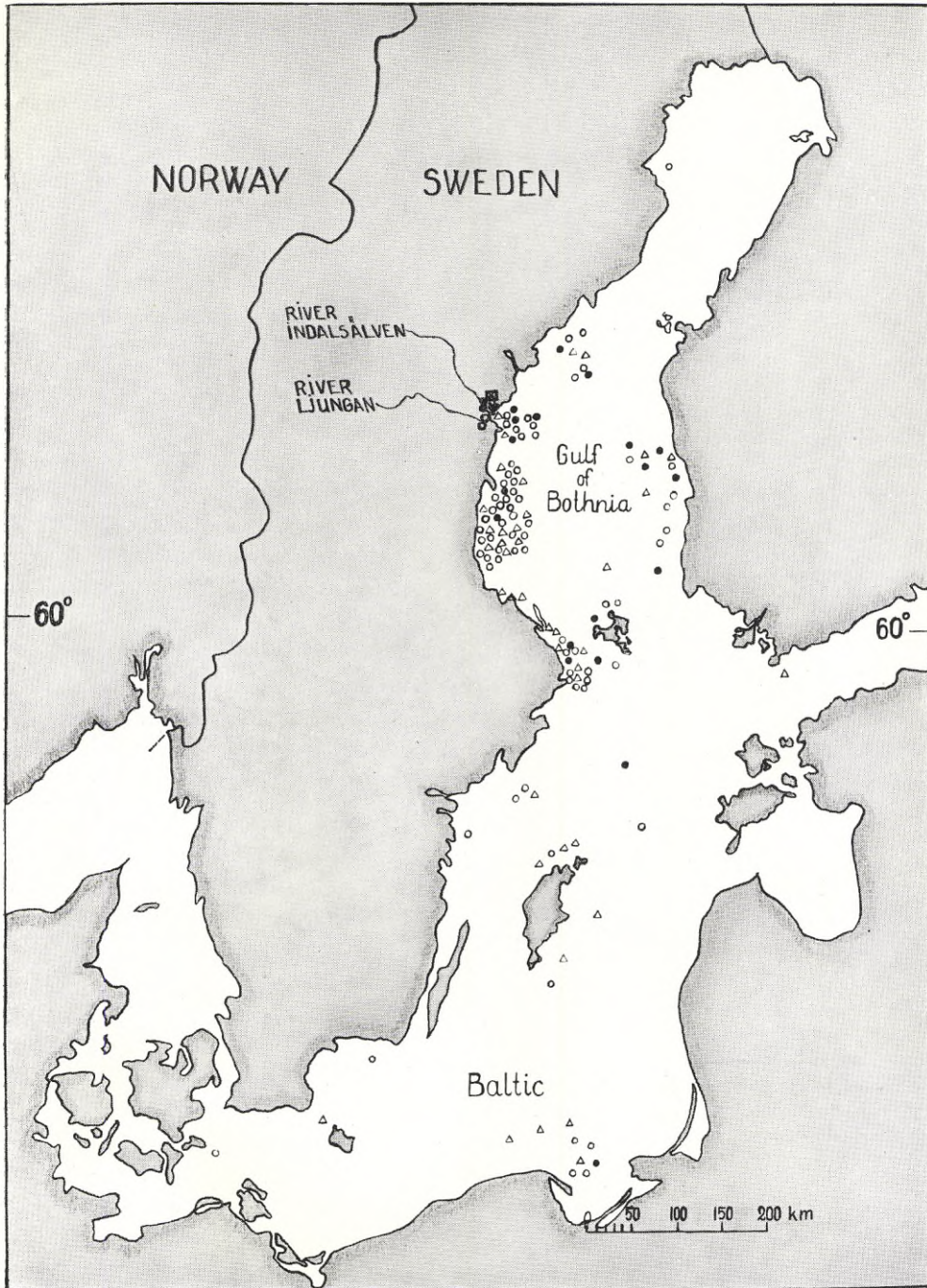| Age in summers	S × St						St × S						S × Bt			Bt × S		
	Exp. 1			Exp. 4			Exp. 16			Exp. 21			Exp. 30			Exp. 35		
	♂	♀	Im.	♂	♀	Im.	♂	♀	Im.	♂	♀	Im.	♂	♀	Im.	♂	♀	Im.
3	1	0	14	2	0	438	0	0	91	0	0	436	0	0	437	6	0	20
4	7	1	7	19	0	274	0	0	59	1	0	428	44	2	154	1	0	4
5	4	1	3	48	3	162	1	0	51	22	6	360	69	1	83			
6	3	1	3	24	12	19	0	0	20	12	5	33	50	19	63			
7	—			—			—			—			12	35	2			

Fig. 4. Map showing recaptures of tagged 6-year-old Salmon (○) and 5-year-old Salmon×
Seatrout (●) and Seatrout×Salmon hybrids (△).

Table 10. Results of tagging experiments with 5-year-old Salmon hybrids and
6-year-old Salmon. (Returns up til November 1955.)

Spec	Number tagged	Number of recaptures					Number of recaptures in percentage of number tagged
		Near to the tagging place	In rivers	Gulf of Bothnia	Baltic	Total	
S × St	136	30	2[1]	17	3	52	38.2
St × S	318	22	—	26	15	63	19.8
S	565	99	2[2]	50	25	176	31.1

[1] River Indalsälven.
[2] River Ljungan.

case in the Salmon and Sea trout the smolt stage in the hybrids is connected
with size to a great extent. In spite of the Sea trout having a better rate af
growth than the Salmon, it first reaches the smolt stage at a somewhat greater
length and higher age than the Salmon.

As far as the hybrids are concerned, at the age of two years in the
experiments, where growth was relatively good, more than 50 % of them
have become smolts, while with poor growth no specimen reached that stage.
No demonstrable dissimilarities between the two hybrids have been found,
but the attainment of the smolt stage seems most reminiscent of the Salmon.
The Salmon×Brown trout hybrids have reached the smolt stage first at a
higher age and greater length. Even at 4 years of age and with a mean
length of 17—19 cm only approximately $^1/_3$ of these hybrids had assumed
the silvery lustre. The Brown trout×Salmon hybrids have, on the other
hand, become silvery earlier.

A good many of the Salmon hybrids have become sexually mature. Table
9 shows the ages for this. At an age of 2 summers no hybrid has become
sexually mature, and at 3 summers only a few males. At a higher age the
number of sexually mature Salmon×Sea trout hybrids has been greater in
the experiments where growth was better, which may be clearly seen by
comparison with Table 7. In the Salmon×Brown trout hybrids sexual
maturity has occurred earlier, in spite of their size having been smaller. At
4 summers and with a mean length of 17—18 cm, only 1 specimen or 0.2 %
was sexually mature of the 428 Sea trout×Salmon hybrids, while 46 speci-
mens or 23 % out of 200 Salmon×Brown trout hybrids of the same age
and length had reached sexual maturity. In all the experiments the males
have become sexually mature earlier than the females. It may be mentioned
for comparison, that with 3-summers-old salmon with a length of 12—14 cm.
in several experiments 10—20 % consisted of sexually mature males, while
with Sea trout of the same age but larger size, approximately 20 cm long,
only a few isolated specimens were sexually mature. Thus the hybrids seem

to have been intermediate. Sexually mature females have, except in a few isolated cases, both in the hybrids and in the parents, first been found at an age of 5 to 6 years.

The sexual products in the hybrids have, however, generally had a structure diverging from the normal. The milt has been very thin, often watery and light in colour. The eggs seemed in many cases to be entirely lacking in yolk and consisted only of an empty shell. In a number of cases, however, the sexual products have seemed to be of a normal character. As was mentioned above, the numerous fertilization experiments have, however, yielded no results or by way of an exception given just a few fry, which soon died.

A considerable number of 5-year-old hybrids of Salmon×Sea trout and Sea trout×Salmon were tagged and released in the spring of 1954 outside the mouth of the River Indalsälven (Gulf of Bothnia). The object was to discover the extent of the migratory instinct. Table 10 shows the results in recaptures of these transplantations and Figure 4 the places, where they were caught. As may be seen, numerous hybrids have undertaken long migrations both in the Gulf of Bothnia and in the Baltic itself. The size of the Salmon×Sea trout hybrids has been 25—35 cm when released and in the reverse hybrids 20—30. cm. After already six months in the sea they had reached a size of 45—55 and 40—48 cm respectively and a corresponding weight of 1—2 and 0.8—1 kg respectively. In the table and figure the recapture results of a simultaneous tagging and release of 6-year-old Salmon reared in ponds are given for comparison.[1] Here the percentage of recaptures lay between the percentage figures for the hybrids. Their size on being released was 30—38 cm and after six months 1.7—2 kg. Thus they were somewhat heavier than the Salmon×Sea trout hybrids wich were one year younger and a little smaller when released.

Results have been poor when releasing fry and one-summer-old or sometimes even older specimens of Salmon hybrids in several small lakes at Kälarne. Only a few isolated specimens have been recaptured, and their rate of growth has not been particularly high.

The Brown trout, Char and Brook trout hybrids.

Table 11 shows the mean length at the end of the first summer of hybrids and in certain cases of the parent fish as well. It appears from this, that the rate of growth in the hybrids generally is intermediate between the parents but most nearly approaches that parent, which had the best growth. In many cases it has been better. Figures 5—8 show some examples of the size

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[1] The figures are from Memoranda Nos. 7 (Lindén) and 9 (Carlin) 1955 from the Migratory Fish Committee (not printed).

Table 11. Mean length in cm in one-summer-old Trout, Char and Brooktrout hybrids and parent fish.

Year	Bt	Ch	Bkt	Bt×Ch	Ch×Bt	Bt×Bkt	Ch×Bkt	Bkt×Ch	Ch×Bkt F 2	(Ch×Bkt)×Bkt
1939	5.1 650[1]	6.3 890	10.0[3] 670	6.4 220	6.2 425	8.5[3] 140	—	—	—	—
1944	5.3 2,100	6.7 925	5.5 1,130	—	7.2 240	5.8 170	—	—	—	—
1944	6.7[2] 64	7.2[2] 297	—	—	7.3[2] 244	—	—	—	—	—
1944	5.5[2] 205	—	6.8[24] 204[4]	—	—	6.8[24] 204[4]	—	—	—	—
1945	4.7 640	—	8.6[3] 360	—	—	9.4[3] 40	8.4[3] 350	—	—	—
1945	6.5[25] 96	6.6[25] 254	—	—	7.2[25] 180	—	—	—	—	—
1945	6.3[2] 14	6.4[24] 580[4]	—	—	6.4[24] 580[4]	—	—	—	—	—
1949	5.5 1,300	—	8.0 800	—	—	—	—	—	?[3] 300	7.2 400
1950	—	7.9 1,260	—	—	—	—	—	—	6.1 460	6.9 1.280
1952	5.2 530	6.3 740	—	6.3 660	6.2 580	—	6.4 780	5.6 770	—	—
1952	—	5.9[2] 205	6.2[2] 260	—	—	—	—	6.6[2] 270	—	—
1954	7.2[6] 1,000	—	—	—	—	—	—	—	9.6[6] 1,090	—

[1] Number of fish obtained.
[2] The three species in the same trough.
[3] Reared in ponds.
[4] The two species not separated.
[5] From Svärdson (1949).
[6] Very different in size.

variation. In these cases as well it is usually somewhat greater in the hybrids than in the parent fish.

In Table 12 are given figures for the number and mean length of the hybrids with continued rearing. As was the case in the Salmon hybrids, mortality has been relatively high in the Trout×Char and Trout×Brook trout hybrids. On the other hand the Char×Brook trout hybrids reared in the ponds at Kälarne have shown lower mortality than specimens of the same size of Char and, in certain respects, of Brook trout as well. During the first year, the rearing of both the Char, Brook trout and hybrid fry (especially the first-mentioned) has gone comparatively well in the troughs at Kvarnbäcken with their cold water (Table 5). When the Char have grown bigger, being stenothermal and cold water fish they do not seem to stand the warmer
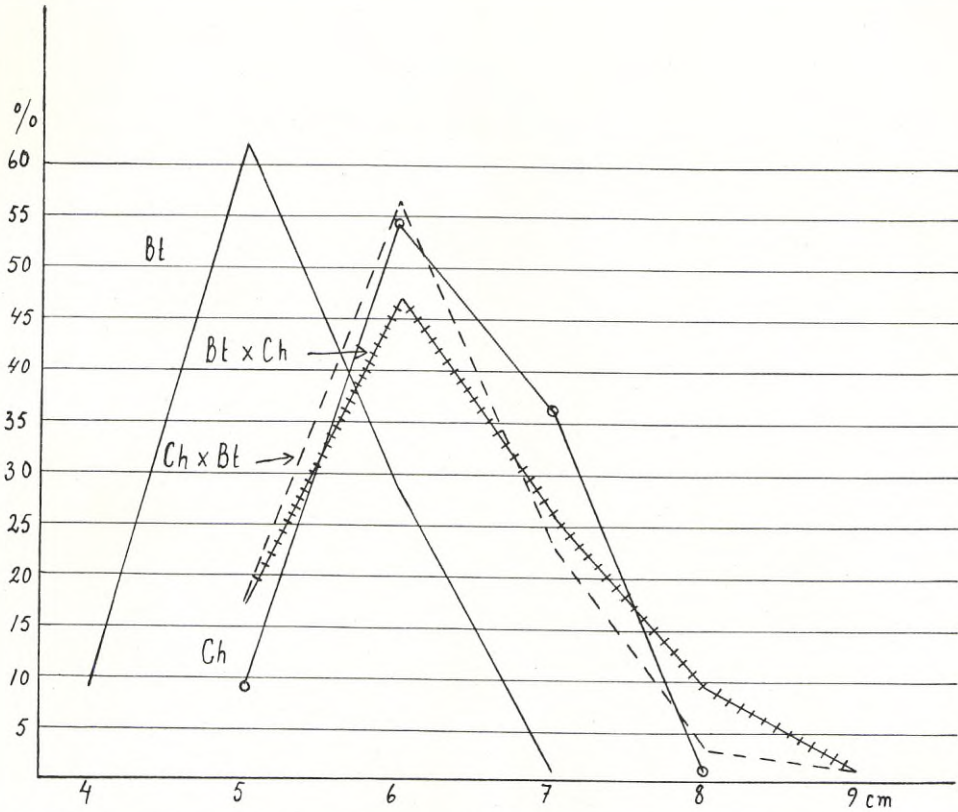
Fig. 5. Size distribution of one-summer-old (1952) Browntrout, Char, Trout×Char and Char×Trout hybrids.

water in the ponds so well. The Brook trout, on the other hand, stands it relatively well. Clearly this hardiness against higher temperatures has been inherited by the hybrids. With increasing age these have also shown lower mortality than the Brook trout. In every case during the experiments at Kälarne the latter have not attained as high an age as the hybrids.

Growth in the different hybrids discussed now has been varied, often better than was achieved in similar rearing experiments with the parent fish. Fry released in lakes have also shown a good rate of growth in the first years. At the age of 2 and 3 summers respectively the recaptured Char×Brown trout hybrids have thus reached a length of 17—25 and 26—39 cm respectively. Char ×Brook trout hybrids have at a corresponding age been 15—27 and 17—38 cm respectively and Brook trout×Char hybrids respectively 10—24 and 20—25 cm long.

The appearance of the Brown trout×Char and reverse hybrids differs very much from that of the parents. The dark bars display a very distinct intermediate form in the young fish (Pl. I d) often up to almost two years of age.
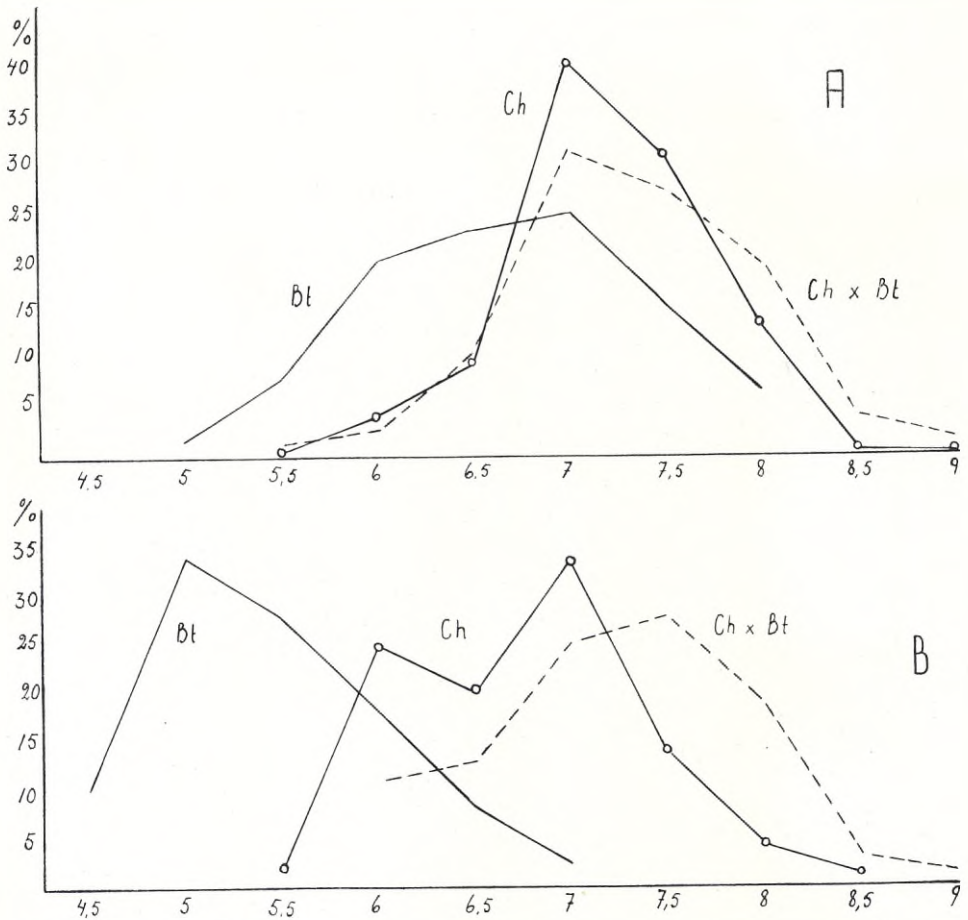
Fig. 6. Size distribution of one-summer-old (1944) Browntrout, Char and Char×Brown-trout hybrids. A. All three spec. reared in the same trough, B. in different troughs.

In the Brown trout they are narrow and high, often rather irregular, but lying in a row. In the Char they are wide, more rounded, often one or more lying more to the underside. In the hybrids they are usually lying in a row, but are considerably wider than in the Trout. The lighter parts round these bars are more clearly demarcated than in the parent and seem to go in loops down between the bars. At a higher age (Pl. II a—c) these darker and lighter parts develop into a sort of vermiculation on a dark ground, which is extremely characteristic and makes the hybrids easily distinguishable from the parents. This vermiculation, which in larger specimens covers the entire flanks, can at times be indistinct and the fish are then shining silver with a faint pink tone. The vermiculation also varies so that the light loops are sometimes very narrow, in other cases considerably wider.
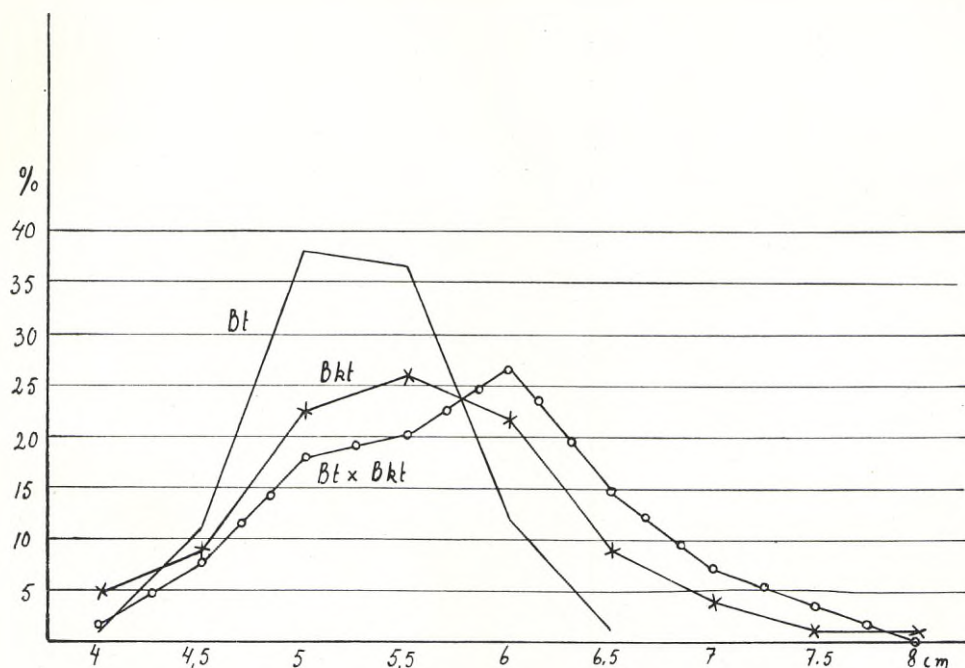
Fig. 7. Size distribution of one-summer-old (1949) Browntrout, Brooktrout and
Trout×Brooktrout hybrids.

The fins of the Brown trout are more or less dotted with dark spots, often
with a narrow black and white edge especially on the ventral and anal fins.
In the Char they are lighter in colour, sometimes with white edges on the
above-mentioned fins. The fin colouring in the hybrids is most strongly
reminiscent of that of the Char, even if a slight spottedness often occurs.

No marked differences in appearance, depending on which of the parents
is the female, have yet been discovered. Possibly the Trout×Char hybrids
are somewhat darker than the reverse hybrids. In the smaller and medium-
sized specimens even the sexes are alike, at spawning time as well. In the
larger and older hybrids the males have, however, a stronger colour marking
and a slight bend on the lower jaw.

The Trout×Brook trout hybrids (Pl. I e and II d) have on the whole a colour
marking, which is strongly reminiscent of that of the above mentioned hybrids.
Most highly characteristic of them is the pale vermiculation, which is perhaps
still stronger here than in the Trout×Char hybrids. The colour marking also
varies in the Trout×Brook trout hybrids. In the larger specimens it is some-
times more a reddish yellow tint and they then have bright red, white-edged
fins. Others, though, are more greyish red with pale pink or almost grey
fins without a distinctly coloured edge.

The one-summer-old Char×Brook trout hybrids (Pl. I f) display, like the
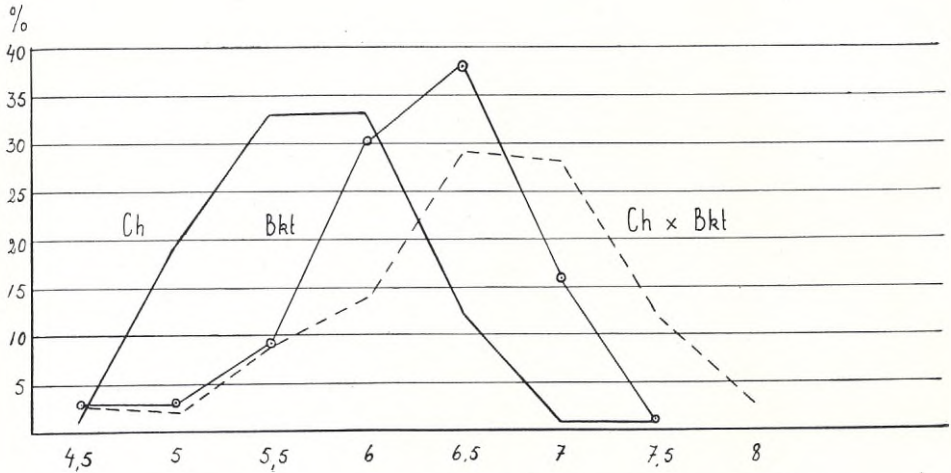
3

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Fig. 8. Size distribution of one-summer-old (1952) Char, Brooktrout and Char×Brook-
trout hybrids.

ones described above, a certain intermediate colour marking, but they are
far more difficult to distinguish from the parents. The form of the dark bars
is more reminiscent of that of the Char than the Brook trout. Certain lighter
crescent-shaped parts above and between the bars in the Brook trout are
united in the hybrids to form more irregular marks, at times also appearing
along the lower edges of the bars. The dorsal fin, which in the Brook trout
usually has a couple of rows of black spots, has only faintly visible rows of
spots in the hybrids. Larger specimens of these hybrids (Pl. II e and III a) still
have an intermediate colour marking. The light spots on the sides are smaller
and more sparse than in the Brook trout and more closely resemble those of
the Char. They also lack the bluish circles typical of the Brook trout. Along the
back, where the Char has a more uniform dark colour while the Brook trout
has a lighter vermiculation, the hybrids have light oblong spots, pointing
in different directions. The pale vermiculation in the Brook trout has, so to
speak, been divided up into a number of separate parts. The dorsal and
caudal fins often have lighter spots or bands on a dark ground and usually
lack the dark marking of the Brook trout. The ventral and anal fins, on the
other hand, are most reminiscent of those of the Brook trout, that is to say
they have distinct black and white zoned edges. In the older specimens the
entire body colour, especially in the males, is more reddish yellow, while
in the case of the Brook trout it is more pink.

In the offspring of hybrid females recrossed with Brook trout males the
colour is more varied (Pl. III d, e). In the majority of cases the number of light
spots on the sides is greater than in the F 1 hybrids, that is to say like the
Brook trout. Sometimes these spots on the sides are sparser, bright pink and

surrounded by narrow circles with a greenish-blue opalescence. The older males in this recrossing have often an oblong white spot with dark edges on the belly, while the females are more yellowish red. The unripe fish are lighter in colour as is the case with the F 1 hybrids. The F 2 hybrids are more variable in appearance than are the F 1 ones, and many of them much resemble on brook trout (Pl. III b, c).

As far as can be ascertained, when going through the Brown trout×Char and reverse hybrids every autumn, no such fish has been found to be fully ripe. In any case, in spite of thorough examination, they have not had normal running spawn or milt. Several of these hybrids of varying size and at the age of three and four summers have been more closely examined (Table 13). In the majority of cases the gonads could only be observed as two extremely narrow, 6—12 cm long threads reminiscent of undeveloped testicles. No differentiated sperm tissue could be observed on microscopic examination. In certain cases, however, a shorter 1.5—3 cm long thickening up to 4—5 mm wide with a distinct, but not normal, sperm tissue has been found on one or occasionally on both of the gonads. It is not possible to say whether or not normal sperm formation has taken place in these cases. Judging by the large number of males the Trout×Char crossing seems, in this case to have produced a certain predominance of males. In one specimen a female gonad was found on one side 4—5 cm long and 5—6 mm wide. Yet microscopic examination revealed only stunted egg cells. Only in a few of these could typical cell nuclei be observed. In lakes recaptured 3 and 4-summers-old Brown trout×Char and reverse hybrids, released as fry, comparatively well-developed male gonads have been found in some cases, although not with ripe milt. Trout females with rather big eggs have been found in the Char× Trout hybrids. It cannot be concluded from this, however, that these specimens were capable of fertilization.

As regards the Brown trout×Brook trout hybrids, no specimens have been obtained of these either with fully developed normal sexual products. Numerous specimens have, though, had clearly formed male gonads and emitted a runny, pale grey, watery milt. In the 5-summers-old specimens of these hybrids, some males have even had a slight but quite definite bend on the lower jaw and in other respects as well have shown certain signs of spawning colouration. In these hybrids as well, the males have been in the majority. Only one definite female could be discovered, a specimen of approximately 35 cm, which had clearly formed, although rather small ovaries with very few eggs 1—2 mm diameter. At the age of 6 summers, when 20 of these hybrids were still alive (length 35—48 cm), none of them yielded spawn or milt.

For comparison it may be mentioned, that in the Brown trout f. l a c u s t r i s sexual maturity usually occurs at an age of 3—5 summers in the males and about a year later in the females. The form f a r i o becomes sexually mature

Table 12. Browntrout, Char and Brooktrout hybrids. Number

Age in years	Bt × Ch				Ch × Bt						Bt × Bkt			
	Exp. 53		Exp. 54		Exp. 56		Exp. 57		Exp. 59		Exp. 61		Exp. 63	
	N	Ml	N	Ml	N	Ml	N	Ml	N	Ml	N	Ml	N	Ml
1	103	9.3	390	7.0	189	7.6	330	7.2	345	7.0	115	11.5	110	6.8
2	68	16.8	285	12.2	96	15.6	87	13.1	82	12.7	88	18.4	18	14.2
3	55	21.8	245	18.6	85	21.8	15	15.1	60	18.8	77	26.1	7	17.7
4	36	29.2	55	22.0	16	28.3	6	20.2	—		32	35.7	7	20.8
5	29	32.5	—		8	30.5	10	29.3	—		21	38.9	12	27.5
6	2	40.9	—		4	37.0	6[1]	34.4[1]	—		20	41.5	12[1]	34.4[1]
7	2	45.5	—		—		6	39.4	—		8—43.4		10	39.4
8	—		—		—		—		—		—		—	
9	—		—		—		—		—		—		—	
10	—		—		—		—		—		—		—	

[1] The two kinds of hybrids were no separated.

1—2 years earlier. When rearing Char 15—20 % of ripe males have been found in certain cases at a length of 15—25 cm and an age of 3—4 summers. In the Brook trout sexual maturity occurs at a still smaller size and lower age. At a length of approximately 30 cm the majority of both males and females are usually sexually mature (in one experiment with 96 specimens, 34 males and 46 females).

Contrary to the Brown trout hybrids the Char × Brook trout hybrids in all the experiments became sexually mature and yielded eggs and milt suitable for fertilization (see Table 1). The latter has, however, been of an unusually hard consistency in the hybrids (exp. 72), instead of fluid as normally. Fertilization experiments with these males have, therefore, been very difficult to carry out. In another experiment (exp. 73) the milt was, however, of a normal nature, and the males could be used quite simply for new fertilization experiments. Sexual maturity has occurred in the males sometimes as early as an age of two summers and a length of 12—14 cm, in other cases, however, it occurred later. In 319 three-summers-old specimens, 43 males and 43

Table 13. Number of Trout×Char* and Char×Trout** hybrids in different stages of sexual maturity.

Length in cm	Sex uncertain. Gonads undeveloped.	Males		Females	
		The one gonad as a small sac.	Both gonads with milt	Very small egg cells stunted	Rather well developed gonads
From ponds { *16—20[1]	4	3	1	—	—
*21—24[2]	3	4	2	1	—
From lakes { *25—30[1]	3	3	1	—	—
**29—33[2]	1	—	—	6	2

[1] Three summers old.

[2] Four summers old.

(N) and mean length in cm (Ml) at different ages.

Ch × Bkt				(Ch × Bkt) × (Ch × Bkt)						(Ch × Bkt) × Bkt				Bt	Ch	Bkt
Exp. 72		Exp. 73		Exp. 75		Exp. 77		Exp. 79		Exp. 80		Exp. 81		Commen length		
N	Ml	N	Ml	N	Ml	N	Ml	N	Ml	N	Ml	N	Ml			
380	9.1	610	7.3	140	—	310	7.0	745	11.7	295	7.2	560	7.8	4—6	5—7	5—7
206	12.6	430	13.2	11	9.5	53	10.0	542	17.8	101	14.7	395	9.8	9—11	10—12	13—16
204	21.1	319	18.3	—		—		—		104	17.6	195	17.3	16—18	17—19	18—20
174	29.4	137	25.2	—		—		—		77	28.9	151	24.5	25—28	22—26	25—30
152	?	—		—		—		—		65	33.5	85	30.0	—	28—30	38—40
133	38.7	—		—		—		—		36	38.6	47	34.8	—	—	—
119	41.2	—		—		—		—		13—39.2		—		—	—	—
52	46.3	—		—		—		—		—		—		—	—	—
38	?	—		—		—		—		—		—		—	—	—
19	48.9	—		—		—		—		—		—		—	—	—

females were sexually mature. With a length of 25—30 cm and at an age of 4 summers, the number of sexually mature specimens from a total of approximately 200 was more than 50 %, the females being in the majority. Something like the same ratio has been shown by the backcross hybrids. Among 222 4-summers-old specimens of such fish 31 males and 63 females were sexually mature. Consequently here too there was a preponderance of females.

On release and recapture at an age of two summers several Char×Brook trout and reverse hybrids have already been sexually mature too. As 3-summers-old fish and in length of 17—38 cms. 22 males and 16 females were sexually mature out of 50 Char×Brook trout hybrids. Of 43 Brook trout×Char hybrids of the same age and of 20—25 cms length only two specimens were not sexually mature. Both these kinds of hybrids also spawned in the lakes, where they were released. Several cleaned and slightly excavated spawning pits could be observed.

IV. Discussion

Previous hybridization experiments.

The first more detailed accounts of hybridization experiments in the Salmon family have been given by DAY (1884, 1886, 1887). He made such experiments primarily with Salmon and Brown trout but also with Char and Brook trout. Apart from the specific dissimilarities in the parents, he has emphasized different factors, which had a detrimental influence on the results, for example the carrying out of the fertilization, the water supply and the nature of the water etc. He has, however, specially drawn attention to the circumstance, that the crossing of a little female fish, for instance a small Brown trout, with a large male, for example a big Salmon, does not

succeed so well. This was, according to Day, due to the eggs in the smaller female fish generally being of a smaller size and consequently having a relatively small micropyle, through which the spermatozoon from a large male fish cannot enter for mechanical reasons. Quite a number of Day's experiments also show, that fertilization diminishes the greater the dissimilarities between the parents. The losses before hatching can then be very great, while with normal hybridization between Salmon×Brown trout and in a reverse direction they were only 25—30 %. Day succeeded in rearing some of the Salmon×Brown trout hybrids in ponds up to 3 and in some cases 4 years. Some specimens became sexually mature during this time. Day then undertook intercrossing of the hybrids among themselves and backcrossing with one of the parents, though always with negative results.

Similar observations concerning automatic impediments to certain hybridizations of Salmon and Trout have also been made by HOFER (1909). He says straight out, that hybridization between Salmon and Brown trout is only possible with Salmon as the female fish while the opposite crossing does not work: »Übrigens lassen sich Forelleneier von Lachsmilch überhaupt nicht befruchten». Undoubtedly on account of this statement, SVÄRDSON (1945) claims, though without having attempted any hybridization experiments himself, that hybridization between Salmon and Trout is only possible in one direction, namely when the Salmon is the mother. For the reasons given, this only holds good if the female Trout is of a very small size. In such cases, when the parents are more similar, hybridization between Trout×Salmon succeeds very well. This was clearly shown already by DAY, who in his experiments mainly had access to Loch Leven trout, a very large form of *Salmo trutta lacustris*.

DAY's experiments with crossing Salmon×Brown trout were repeated later by JONES (1947). Particulars as to losses and fertilization are, however, not available. On the other hand Jones made a detailed investigation of some similar hybrids reared in ponds (see below). Many of the hybrids had milt and according to JONES's investigations completely active spermatozoa. JONES also found female gonads in several specimens and in one case they were ripe with a few large yellow eggs. He says that he also had specimens of a backcross hybrid, a Salmon×Trout female×a Salmon male for examination, although he had not carried out the fertilization of the spawn himself. This seems, therefore, to be the only known case of a successful crossing of this kind.

Hybridization between Salmon and Trout was regularly carried out, according to FEHLMANN (1926), as early as the latter half of the 19th century in connection with salmon hatching in the Rhine and during the 20th century in the Baltic River Persante as well (HENKING 1929, 1931). This often occurred because male salmon were not available in sufficient quantities, but also for the purpose of combining certain good qualities in the parents,

which was, however, not successful. DAY's experiments were obviously not known, and as far as can be judged, it was only a question of fertilization of Salmon eggs with Trout milt. Further details are lacking regarding the losses during hatching and about the results in general. During the years 1918—1922 FEHLMANN (1926) carried out new experiments and reared the hybrids in ponds to an age of 3 years. The majority were then sexually mature and attempts were made to obtain an F 2 generation. Mortality before the fry stage was however 100 %. During the latter half of the 1920's SCHEURING (1930) undertook experiments with crossing Salmon×Brown trout and reverse. Although complete particulars regarding fertilization and mortality are not to be found in this case either, it is emphasized that the cross Salmon ×Brown trout gave far better results than Brown trout×Salmon. This did not depend, however, on fertilization not having taken place because of the small size of the Brown trout eggs but on the larger number of malformations and more extensive yolk sac disease in the Brown trout×Salmon crosses. The fertilization has thus clearly been successful. The hybrids were kept in ponds for one year, when the largest had reached a length of 20 cm.

Renewed exhaustive experiments with hybridization in both directions between Salmon and Trout, now Sea trout, were made by WINGE and DITLEV-SEN (1948). Here no mechanical impediments to fertilization existed, as they only used 30—40 cm long sexually mature Salmon reared in ponds, while the Sea trout females were approximately 45 cm long. The authors also state, that the fertilization percentage both in the crossing and control experiments was 95—99 %. Details regarding mortality before hatching are lacking, which perhaps indicates that it was not particularly great. However, one month after hatching mass deaths occurred among the hybrids, especially of the cross Trout×Salmon. In these experiments too a number of the hybrids were reared in ponds. Some males became sexually mature and two back-crossing experiments were made between Trout females and S×St males as well as St×S males. The fertilization was rather poor, only 16—20 %, and the embryos displayed big deformities. Mortality was also very high, and only 3 eggs hatched but the fry died before leaving the eggs completely. No sexually mature F 1 hybrid females were obtained. The ovaries in the hybrids were entirely unlike normal ones and consisted predominantly of very small cells among which a few large eggs occurred.

As is evident from the above, the hybrid fry obtained in most of the experiments mentioned were reared in ponds, in the majority of cases, however, only to an age of 2 to 3, sometimes 4 years. At times this seems to have depended on the number having been so small, that it was not considered worth while continuing, in other cases the mortality has clearly been so great, that the hybrids did not grow to be any older. Certain details regarding the appearance and morphology of the hybrids are, however, available. Thus DAY has a number of particulars regarding the size of the

different parts of the body and the colour of his Salmon hybrids. JONES too has provided such descriptions, but also particulars as to the number of scales between the lateral line and the adipose fin, the number of dorsal fin rays and the number of pyloric caeca. The hybrids were more like Trout than Salmon. Certain characteristics were reminiscent of the Salmon, others more like the Trout, while others were intermediary. In DAY's experiments too the Trout characteristics were predominant. Concerning growth, JONES gives this only for a few specimens. As 2-year-olds the length was approximately 22 cm and as 4-year-olds resp. 33 and 34 cm.

WINGE and DITLEVSEN have made very thorough measurements of certain fins and parts of the body in their Salmon hybrids. On account of relative changes in these particulars in connection with the size of the specimens, varying between 6 and 19 cm at an age of 2 summers, no certain dissimilarities from the parents could be established in the hybrids. It is emphasized, however, that the colour marking and the general appearance in both kinds of hybrids, but especially in the Sea trout×Salmon hybrids, were more in accordance with the Sea trout than with the Salmon. The same thing is also pointed out by SHEURING regarding the Salmon×Brown trout hybrids he reared. The Danish scientists in addition observed, as did also HENKING, that the gill rakers were intermediate in the hybrids. In behaviour the Salmon× Sea trout were more like Salmon and the reverse hybrids more like Sea trout (WINGE and DITLEVSEN).

DAY, the pioneer on artificial hybridization experiments, also made such experiments with Trout×Char, Trout×Brook trout and Char×Brook trout (1884, 1886). The losses varied very considerably here. The crosses Brown trout×Char had a mortality before hatching of 99 %, while in the Brown trout×Brook trout and reverse and in Char×Brook trout and reverse during the same period mortality only amounted to 23—32 %. The alevins in the crosses Brown trout×Brook trout and still more the reverse ones were, however, very deformed and displayed a high rate of mortality. The figures for this are not available, but it seems as if the total mortality during the whole period until the liberation of the fry was very high. A number of these hybrids called Zebra fish and Leopard fish were reared, some to an age of 3—4 years. A few specimens then produced milt, which however proved of no use for fertilization. The crosses Char×Brook trout and reverse showed, according to Day, far lower mortality and no deformities worth mentioning in the alevins. The majority of these hybrids became sexually mature as 3-year-olds and were used for intercrossing and recrossing. In the former case mortality was high, 83—99 %, in the latter case less, 63—78 %. A number of F 2 hybrids were obtained and were kept for 3 years.

Hybridization experiments with other species of the Salmon family than Salmon and Trout have also been carried out at the fish-culture institutions of Central Europe and HOFER (1909) has made a special study of them. He

thus points out that hybridization Char×Brook trout and reverse (Elsässer Saibling) was quite common. These hybrids were easy to rear in ponds and did well on liberation in open waters. They are also said to have bred there. Likewise in Brown trout streams, where Brook trout had been released, such hybrids were sometimes to be found according to HOFER. Both HOFER and NERESHEIMER (1937) state that F 2 specimens resembled the parents as far as appearance is concerned. When crossing Brown trout×Char and reverse very heavy losses are substained, according to HOFER, so that only approximately 5 % of the spawn reaches the fry stage. Brown trout×Brook trout crosses are said by Hofer to have up to 99 % mortality rate. BADE (1901—02) declares that it is impossible to produce such hybrids, while on the other hand the reverse Brook trout×Brown trout crossing can be carried out, even if the losses are very great. According to NERESHEIMER (1937), such hybrids called »Tigerfische» have been reared at the above-mentioned fish-culture institutions. This has also been the case in Norway (J. SØMME 1941), where it was intended to use such hybrids for transplantation. The hatching percentage was quite high, but more detailed particulars about this or about the results of the transplantation are not available. It ought also to be mentioned that, according to HOFER, Rainbow trout females (*Salmo irideus* GIBB.) were crossed with Trout males, while the reverse crossing did not succeed.

Finally mention should be made of the results of certain hybridization experiments with Salmon in North America. Apart from the earlier experiments of this type made by *Bean* and *Green* mentioned in the literature (STENTON 1952, FOERSTER 1935) has shown, that hybridization goes relatively well between certain of the Pacific Salmon species, but not with others and that sometimes backcrossing has succeeded as well. Furthermore STENTON (1950) carried out successful crosses between Lake trout (*Salmo* or *Cristivomer namaycush* WALLBAUM) and Brook trout with only small losses. The former hybrids are called Splake trout and have been released in many lakes, where they did well and have also bred. When reared in ponds the hybrids have become sexually mature as 3-year-olds and spawned for several consecutive years. They have then resembled the male parent, while the Lake trout become sexually mature first at 5 to 6 years of age and spawn only every second or third year. The hybrids have also been used for intercrossing to an F 2 generation. The losses among the F 2 hybrids have, however, been much higher than among the F 1 hybrids and the F 2 alevins have also been weaker than the F 1 ones.

STENTON has also given other particular about these Lake trout×Brook trout hybrids. They showed in certain characteristics a similarity to one or other of the parents, but some characteristics were intermediate. Thus of 25 taxonomic measurements and counts 9 were intermediate, while 6 agreed with Brook trout and 10 with Lake trout. The intermediate appearance of several parts of the body has also been shown by SLASTENENKO (1954).

Finally CUERRIER (1954) has pointed out, that several of the excellent qualities in the parents from a fishing point of view have been combined in the hybrids. Certain experiments on the resistance of the hybrids as regards high and injurious temperatures have shown, that even in this respect they were intermediate in relation to the parents (FRY and GIBSON 1953). The F 2 hybrids have, however, according to CUERRIER to a certain extent returned to the colour of one of the parents but some have been typical hybrids.

A hybridization experiment, evidently rather little known in the literature, was made in New Zealand in the 1920's, but was described for the first time by STOKELL (1949). It concerned the crossing of a female Rainbow trout with a male Brown trout. 100 fry were obtained, some being reared up to an age of 2 years. Three specimens were then sexually mature, and an intercrossing experiment succeeded so well, that approximately 1,500 alevins were produced, of which a part were again reared for a couple of years. Some of the specimens examined by STOKELL, whether of the F 1 or F 2 generation he did'nt know, were clearly intermediate as regards certain of the different characteristics in the parents, esp. the number of vertebrae and gillrakers.

Although the Salmon family is not concerned, mention may very well be made here of some further artificial hybridization experiments in fishes. LIEDER (1954) has thus crossed Roach (*Leuciscus rutilus* L) with Bream (*Abramis brama* L), with Rudd (*Leuciscus erythrophtalmus* L) and with Gudgeon (*Gobio fluviatilis* L). No particulars about mortality or the appearance of the hybrids are available. NIKOLJUKIN (1941), who crossed Roach and a species of *Leuciscus* from Southeastern Europe (*L. danilewski* KESSLER) mentions on the other hand, that these hybrids were lively and grew rapidly as well as being intermediate in many respects. This is, as is well-known, the case with the hybrids between Roach and Bream (GEYER 1937) and other species of the Cyprinid Family (HEINCKE 1892) found quite frequently in nature.

Experiments have also been made in America with hybridization between species in the *Cyprinidae* (SCHULTZ and SCHAEFER 1936) but mostly with other different fish species, esp. in the Sunfishes (BAILEY and LAGLER 1938, THOMPSON 1935, HUBBS 1932, 1933, 1943) and the Pike (*Esox*) family (EMBODY 1918, UNDERHILL 1939, BLACK and WILLIAMSON 1946). Many of these experiments have been very extensive and a number of interesting results have been obtained. Thus it has been possible to establish that certain divergent forms of intermediate type occurring in nature are hybrids and not merely variations of certain species, for numerous hybrids produced by artificial hybridization have proved to correspond completely with those found in nature. Furthermore an increased rate of growth as compared with the parent species, several intermediate taxonomic characters, often a heavy predominance of males and generally a total infertility could be definitely

established in the majority of the hybrids. Yet in some Pike hybrid experiments a few females have become sexually mature with fertile eggs, but the male hybrids have probably been sterile.

The literature on artificial hybridization in fishes, of which an account has just been given, does not, with a few exception, touch on the cytological problems. These have only been taken up for examination by SVÄRDSON (1945) and LIEDER (1954). SVÄRDSON has made a thorough study of the chromosomes in a number of species of the Salmon family and has been able to determine their number and in many cases their construction as well. He has also had some hybrids from the Kälarne experiments for investigation, namely Salmon×Brown trout, Brown trout×Char and Brown trout×Brook trout. In short it can be established from SVÄRDSON's work that the diploid number of chromosomes in the Salmon is 60, in the Brown trout and the Char 80 and in the Brook trout 84. The chromosomes of the Brown trout and the Char are, in spite of being the same number, greatly differentiated from one another and the former are more homologous with those of the Salmon. The Brook trout and the Char chromosomes are more in agreement with each other than with the other species. In the Salmon×Trout hybrids SVÄRDSON found a diploid number of chromosomes of 70, in the other two hybrids the disturbances were very great, especially in the hybrid Brown trout×Brook trout and it was not possible to confirm the number of chromosomes. SVÄRDSON also mentions that the chromosome disturbances in the metaphase are greater in attempts to produce an F 2 generation or to recross the F 1 hybrids with one of the parents.

LIEDER mainly intended with his experiments (see page 42) to study the effect of the crossing on the chromosome conditions. He discovered that the diploid number of chromosomes in the hybrids was 52 or the same as in all the species, which were the subject of crossing. In the Roach×Bream hybrids no dissimilarities in the external morphology of the chromosomes as compared with the parents could be shown. In the Roach×Gudgeon hybrids the morphology of the chromosomes displayed certain divergencies in the hybrids.

The Kälarne experiments.

The results from the series of hybridization experiments at Kälarne, of which an account has been given above, have shown that it is possible to produce F 1 hybrids between the majority of species of the Salmon family. Only the experiments with Brook trout×Brown trout, Salmon×Char and Salmon×Brook trout have given entirely negative results. It has also been possible to keep the fry in ponds and in the majority of cases, contrary to the earlier experiments, to rear fully grown hybrids to an age of 10—11 years.

Fertilization and losses before the fry stage.

The figures quoted from the experiments show, that so far as mortality before the fry stage is concerned, hybridization between certain species succeeds relatively well, while the results in other cases are considerably poorer. There have also been very great dissimilarities in mortality within a hybridization series with the same species. It is therefore obvious, that a single hybridization experiment is not sufficient. Here factors, which have nothing to do with the two parents' systematic position, have clearly played a part. Actually observations from all ordinary fish-culture go to show that the eggs — possibly the milt as well — from as far as can be seen similar specimens of the same species of fish can be entirely different with regard to fertilization, mortality and the vitality of the fry. Another important factor, which is of particular significance in hybridization, is the difficulty in obtaining fully ripe specimens of the two species included in a certain experiment, as for example Salmon and Sea trout. The latter usually spawns at an earlier date than the former. Female Sea trout for crossing have, therefore, been retained in ponds until the salmon are ripe to spawn and for the above-mentioned reasons have not always been in the best condition for spawning. On the other hand males of the Sea trout have milt for a longer period of time and have been easier to retain in ponds and use for fertilization of Salmon eggs. Thus at the best time for Salmon to spawn one has perhaps had fully ripe male and female Salmon and similar Sea trout males, while the females of this species have not been so suitable for stripping. This may be an explanation why the results with a crossing Salmon×Sea trout are at times more successful than the simultaneous control experiment with Sea trout×Sea trout. In the experiments with Salmon×Sea Trout and reverse, in which the reverse in a few cases gave entirely negative results, these poor results can probably be attributed to similar causes, namely, the poor fertilisation due to using parent fish in inadequate spawning condition.

The average mortality (30—43 %) in my salmon crossing experiment has been similar to that obtained in DAY's experiment in regard to the Salmon ×Sea trout crosses, but somewhat higher with regard to the reverse cross. There is a possibility that the higher mortality in these crosses may be connected with the fact, that in many experiments the female fish was small compared with the male fish. This should, however, have applied still more in the experiments with Salmon×Brown trout and reverse. Here the Brown trout females were only 40—45 cm long as opposed to the Salmon males of 60—70 cm. Total mortality has occurred, however, in the crosses in both directions in these experiments. It is probable, therefore, that in these cases other factors than the small size of the female fish have been decisive. The same thing occurred in the experiments with crosses Salmon×Char and Salmon×Brook trout and all the intercrossing and backcrossing experiments

with the Salmon hybrids. They have, like similar experiments by DAY, HOFER, WINGE and DITLEVSEN, yielded no results, undoubtedly on account of disturbances in the chromosomes in the metaphase (see below). JONES's statement about a successful result with such a backcrossing, which was not carried out under his own supervision, seems therefore as if it should be taken with reserve. It can, however, be established from what has been quoted above both from previous experiments as well as from my own that the impossibility of crossing Trout eggs with Salmon milt, claimed by some scientists, has only a very limited validity.

Nor can this mechanical factor have played a decisive role in the other experiments. In the experiments with Brown trout×Char and reverse the larger forms of *Salmo trutta lacustris* and *Salmo alpinus* occurring in Lake Vättern and which weigh several kilograms were used. Here the Char has usually been somewhat smaller, and besides the Char also have smaller eggs than Brown trout of a similar size. Should any mechanical fertilization difficulties have arisen in these experiments, it should therefore have primarily been the crosses Char×Brown trout which were affected. The losses have, however, been less here all through than in the reverse crosses. On the whole these experiments have moreover given better results than DAY's.

In all the experiments with Brown trout×Brook trout and reverse as well as Char×Brook trout and reverse the parent fish have been of a comparatively similar size. The total mortality in the experiments Brook trout× Brown trout can thus not be explained by the female fish and its eggs having been too small. The mortality in the crosses Brown trout×Char, 64—80 %, in one case 100 %, corresponds approximately to what DAY and HOFER reported, while BADE considered that this crossing could not be carried out. The most usual crossing in Germany for obtaining »Tigerfische» should thus have been Brook trout×Brown trout.

Probably the purely negative results in my experiments with this hybridization may be explained by the sexual products not having been at the same stage of ripeness. In addition it should be pointed out that the eggs of the Brook trout used at the Kälarne Hatchery were not of the best quality. They have suffered high mortality (Table 3), even in the control experiments.

The mortality in the crosses Char×Brook trout and reverse has been low, 25—50 %, in my experiments as well. On the other hand it has been higher in both the intercrossing in F 2 and the recrossing with Brook trout. This is in close agreement with STENTON's (1952) Lake trout×Brook trout crosses. The European Char and the American Lake trout thus seem to behave similarly on crossing with Brook trout.

All the hybridization experiments now described show that mortality has been higher in the crossed eggs and fry than in the eggs from the parents. In certain cases this can clearly be attributed to the above-mentioned

difficulties in obtaining fully ripe sexual products in both parents as well as, though more seldom, purely mechanical impediments to fertilization. The most important reason for fertilization failing to occur or being poor and for a high mortality throughout in the crossed eggs and fry must of course be disturbances in the chromosome balance in the metaphase. It is therefore of interest to be able to establish, that the different degrees of mortality in the crossed eggs and alevins bear a clear relationship to the above mentioned differences in number and morphology of the chromosomes established by SVÄRDSON (see page 43). Nearest to one another in these respects are Salmon and Trout on the one hand and Char and Brook trout on the other. The lowest mortality in the crossed eggs and fry has been found in the Char× Brook trout hybrids and next in the Salmon×Trout hybrids. The crosses Salmon×Char and Salmon×Brook trout have all failed completely, and the mortality in the eggs and alevins in the Trout×Char and Trout×Brook trout crosses has often been very high.

The ease or difficulty of obtaining hybrids between different species of the Salmon family thus agrees very well with what is known regarding their chromosome conditions. And it also confirms the generally accepted systematic position of the different species with Salmon and Trout on the one hand and Char, Brook trout and American Lake trout on the other.

Fingerlings and fully grown-hybrids.

As has been mentioned above, the Kälarne hybridization experiments have also been aimed at rearing the fry to fully grown fish for the purpose of discovering the mortality, rate of growth, sexual maturity, fertility etc.

Regarding mortality it can be pointed out that both during the first summer as well as during later years, it has been greater in the hybrids than in the parents. In spite of this several of the hybrids attained an age of 7—8 years, certain specimens surviving up to 11 years. Such old hybrids have not been obtained in earlier experiments, as has already been mentioned.

Growth during the first year has been good throughout, usually intermediate in such cases, where one of the parents normally showed a poorer rate of growth than the other, as in the Salmon and Trout. In many cases growth has, however, been at the same rate as in the fastest growing parent, at times even better. This is the case, for example, in the majority of the Trout, the Char and the Brook trout hybrids. In certain cases the hybrids and the parents have been reared in the same trough. Here the competitive conditions could play a part and perhaps entailed both retarded growth as well as larger losses in the parent normally displaying the poorest rate of growth. This has been particularly the case with the Brown trout both in experiments with Char and the hybrids Trout×Char (compare SVÄRDSON 1949 b) as well as with Brook trout and the hybrids Trout×Brook trout.

Table 14. Mortality from fry to yearling stages, mean length in cm (Ml) and size variation S.v. = (Number of 0,5 cm groups) in experiments with one-summer-old hybrids and parent in the same trough.

Year		Bt	Ch	Ch $\times$ Bt
1944	Number of fry	330	330	330
	Number of yearlings	64	297	244
	Ml.	6.7	7.2	7.3
	S. v.	6	6	7
1945[1]	Number of fry	500	500	500
	Number of yearlings	96	254	180
	Ml.	6.5	6.6	7.1
	S. v.	8	5	8
1945	Number of fry	500	500[2]	500[2]
	Number of yearlings	14	580	
	Ml.	6.3	6.4	
	S. v.	5	9	
		Bt	Bkt	Bt $\times$ Bkt
1944	Number of fry	330	330[2]	330[2]
	Number of yearlings	205	204	
	Ml.	5.5	6.8	
	S. v.	5	9	
		Ch	Bkt	Ch $\times$ Bkt
1952	Number of fry	300	300	300
	Number of yearlings	205	260	270
	Ml.	5.9	6.2	6.6
	S. v.	6	6	7

[1] From Svärdson (1949).

[2] The two spec. not separated.

It has previously been pointed out that the variation of the size groups in the one-sommer-old hybrids (the difference between the shortest specimen and the longest one) has often been greater than in the parents. This holds good both when the different species are reared in the same trough, as well as in other cases. Only with simultaneous rearing, however, can a comparison be made in this respect.

In Table 14 figures from Tables 5 and 11 have been grouped to show both the size and size variation as well as the mortality in such experiments. SVÄRDSON (1949 b) has made the suggestion that size variation should be connected with competition for food, becoming, for certain reasons, greater the smaller the number of captured specimens of a certain species. Some curious circumstances then arise, which are very difficult to explain. Thus, for example, that a poorer rate of growth is often found in the species in which the losses were the heaviest. One would expect a better rate of growth there, if it was only a question of intraspecific competition. As was pointed

out in the introduction, the varying numbers do not seem to have had any greater influence on growth owing to the regular and plentiful supplies of food provided in these troughs. Table 14 also shows that in the present experiments no correlation is to be found between numbers and variation in individual size. It is clear on the other hand, as previously mentioned, that the size variation is greatest in the hybrids.

In certain experiments with Sunfish hybrids KRUMHOLZ (1949) has shown that growth has been somewhat better and the condition factor higher, when such hybrids have been reared separately, than when they have been reared together with other fish. There the interspecific competition has clearly had a more deleterious influence on growth than the intraspecific one. Unfortunately my experiments have not been planned so that they could shed light on this question, which is very interesting in itself. On the whole the question of the correlation between growth, competition and mortality, especially in the hybrids, ought to be the subject of more detailed experiments.

As regards continued growth in the hybrids now discussed, it has been very good both in ponds and in lakes, where they were released. In no case have they displayed backwardness in this respect. This is in accordance on the whole with what is known from hybridization experiments both with fishes and with other organisms (BAILEY and LAGLER 1938, BLAIR 1954, HUBBS 1932, 1933).

The Kälarne Salmon hybrids confirm the results previously obtained with regard to appearance. Both the number of the darker spots and the colour of the fins have been more like Trout than Salmon. This is especially the case with regard to the spots in the Salmon×Brown trout hybrids. The stronger colour marking in the Brown trout thus seems to be passed on as a dominant. On the other hand the often more evenly demarcated dark parr marks in the Salmon have been very distinct in all these Salmon hybrids and in the Salmon×Brown trout hybrids have still been found even in the older specimens.

Regarding the time at which the smolt stage is reached, the hybrids between Salmon and Sea trout have corresponded to the parents and principally to the Salmon. In the Salmon×Brown trout hybrids the circumstances have, however, been different. The form of Brown trout f. *fario* crossed in this experiment is mostly rather stationary, not undertaking any migration and therefore not coming as a rule into the silvery smolt stage either. It is interesting, therefore, to find that among the hybrids only a minority became as silvery as the Salmon smolt, while the majority retained the colour marking characteristic of the Brown trout f. *fario*. These hybrids have not, therefore, reached a smolt stage, in spite of an advanced age.

With regard to the Salmon hybrids, attention should finally be drawn to their having undertaken long migrations on being released at the coast. In this respect they have resembled the Salmon, as the Sea trout, at least in

the Baltic and its bays, does not undertake any such long migrations. This strong migratory instinct has been clearly found in both the Salmon×Sea trout and in the reverse hybrids.

The Brown trout×Char and reverse hybrids and the Brown trout×Brook trout hybrids are, unlike the Salmon hybrids, entirely dissimilar to the parents in appearance. Even if the ground-colour varies very much from dark brownish green to light rose or almost silvery, all these hybrids display a very characteristic pale vermiculation on a darker ground. In this respect they differ very considerably from both the parents. It is strange, that almost the same colour marking can be obtained when crossing Brown trout with Char and with Brook trout, two species which differ considerably from one another in appearance. But clearly the factor for dark colour marking on a light ground in the Brown trout reacts particularly strongly and at the same time similarly in crossing with the factor for lighter colour marking on a dark ground, which is found in both the Char and Brook trout. These species are, as previously emphasized, closely related systematically. Nor does the appearance of the Char×Brook trout hybrids, which as far as colour marking is concerned is quite intermediate, differ very noticeably from the parents. It is also very reminiscent of the appearance of STENTON's (1952) Lake trout× Brook trout hybrids.

The development of the gonads as well as sexual maturity and capacity for inter- and backcrossing have been most nearly normal in the Char× Brook trout hybrids. These hybrids, like STENTON's mentioned above, spawned in the lakes, where they were liberated, and then displayed the same behaviour as the parents, that is to say they made spawning pits, where the bottom material permitted. Nearest to these hybrids come the Salmon× Trout hybrids as regards the stage of sexual maturity. The majority of them have had well-developed eggs and milt sacs and in many cases ejected apparently normal milt and at times even eggs. The constant negative results obtained by me and with one exception (JONES 1947) also by earlier authors in inter- and backcrossing experiments indicate, however, that the dissimilarities in both the parents' chromosome conditions are too great normally to permit the development of an F 2 generation or a backcross with either of the parents. The latter is particularly the case in the female hybrids. It is possible that crossing of eggs from Salmon or Trout with milt from a hybrid can succeed better than the only experiment of the kind (45) showed.

Finally in the very dissimilar Brown trout×Char and Brown trout×Brook trout hybrids no fully ripe sexual products could be obtained, even if in a number of cases the gonads were well-developed. No inter- and backcrossing experiments could thus be carried out. This corresponds with the experiments with these species of fish mentioned in the European literature and is also in agreement with the results of HUBB's (1932, 1933) experiments on hybridization with different species and genera of sunfishes. HUBBS admittedly found a

few males from which milt could be stripped and also some females with eggs, but the fertilization failed. Similarly to BAILEY and LAGLER (1938) HUBBS also found a heavy predominance of males in the hybrids. This seems also to be valid for the Brown trout×Char hybrids examined by me.

The remarks made regarding the appearance, the sexual maturity and the fertility in the different kinds of hybrids further confirm what has been said above on the systematic position of the species Salmon, Brown trout, Char and Brook trout.

V. Hybrids in the Work of Fish Conservation and in Nature

It was pointed out in the introduction, that artificial hybridization between species of the Salmon family could be of both theoretical and even more of practical interest. Only the latter question will be touched upon here.

First regarding the Salmon×Sea trout hybrids there seems to be no reason for producing them. If for some cause larger male Salmon are not available, Salmon parr can very well be used, as has been learnt from direct experiments (ALM 1943) and other investigations (JONES and KING 1952). There is, therefore, no reason in such cases to use Sea trout males.

The reverse hybrids Sea trout×Salmon can perhaps be of more interest. As is well-known, Salmon do not spawn in Sweden in the majority of small rivers, where the Sea trout go up for spawning. Here it would be valuable to test whether Sea trout×Salmon hybrids could be introduced. The earlier appearance of the smolt stage in these hybrids as compared with the Sea trout might perhaps give rise to an earlier emigration with subsequent increased growth in the sea commenced at a lower age. Possibly a tendency inherited from the Salmon towards better growth than in the Sea trout may be found in these hybrids.

The Salmon×Brown trout hybrids have not displayed any characteristics, which speak in favour of a production of such hybrids having any practical value. The Brown trout has a good rate of growth and is relatively stationary under favourable environmental conditions. Numerous hybrids would perhaps emigrate instead and disappear from their native place. If a shortage of Salmon eggs should arise for some reason, however, when a supply of Brown trout eggs was available, artificial hybridization with Salmon males could possibly bring about a better rate of growth and an addition to the population of Salmon in the sea. It must be remembered, however, that the losses in the first stages of life in these Salmon hybrids are greater than with intraspecific fertilization.

This is still more the case for the Trout×Char and Trout×Brook trout hybrids. The production of such hybrids can, of course, be of great interest, if it is a question of showing or in a certain water having such entirely dis-

similar and beautiful fish. As these hybrids can quickly be distinguished from the parents even by a fisherman, they ought in themselves to be of use for testing the value of fish culture in water, where one or both of the parents are already to be found. The greater mortality in the growing hybrids shows, however, that they are not as robust as the parents. The survival value of the hybrids in nature must thus be rather uncertain. They cannot, therefore, be considered suitable for testing the value of fish culture.

The Char×Brook trout are the hybrids having the greatest practical interest of those under consideration. They have shown themselves to be more resistant to high water temperature than the Char and they seem to live longer than the Brook trout. They have in addition a good rate of growth and are fertile. Mortality in the egg and alevin stages is not as great either in these hybrids as in the others, so it is easy to obtain them in large quantities. Perhaps they would on that account be suitable for releasing in waters, where at all events the Char does not do well.

The colour and appearance in these hybrids are, as previously mentioned, not so dissimilar from the parents as is the case with the Trout×Char hybrids. It is not impossible, however, for an observer with some training to distinguish in every case the F 1 hybrids from the parents. Bearing this in mind and taking into consideration the rather low mortality, these hybrids could consequently be used for testing the value of fish culture.

In this connection it is of interest on the basis of previous results and those now presented to touch on the question of the possibility of the origin in nature of the hybrids discussed here. Regarding the general prerequisites for natural hybridization in fishes or for the avoidance of the same, several scientists and in particular BLAIR (1954) have emphasized such factors as the systematic relationship and morphological differences of the species, ecological isolation, different places and times of breeding, the existence of pairing acts and different courtship patterns. Natural hybridization should not, for example, take place so easily in species, in which there are more or less permanent pairing and care of the progeny. Another factor, which can also have an effect and which can for example be the reason for the varying occurrence of natural hybrids in the Cyprinid- and the Salmon families, is mentioned by HUBBS (1933) namely crowding of a population and reduction of available spawning sites. HUBBS has found that this factor is responsible for hybridization in some populations of Sunfishes. BAILEY and LAGLER (1938), who also studied these conditions in the Sunfish, have found in one particular case such a general natural hybridization that the hybrids amounted to 11.7 % of a large sample. Among certain populations of Suckers HUBBS has found up to 6 % consisting of natural hybrids.

It is natural, for the above-mentioned reasons, that hybrids easily come into being in species of the Cyprinidae, which usually collect in large quan-

tities for spawning, have scarcely any real pairing (compare also SVÄRDSON 1949 a) and appear in many waters in crowded populations.

In these respects the above-named species of the Salmon family differ markedly. They do not appear in large quantities on the spawning grounds, they only occur very occasionally in crowded populations and they have in addition marked courtship and pairing acts (JONES and KING 1952, FABRICIUS 1952). Such hybrids are seldom mentioned in the literature, probably often because they are difficult to recognize from the parents. This is primarily the case in the Salmon×Sea trout hybrids. Actually these two species are sometimes difficult to tell apart with any certainty at a hasty glance. It is therefore natural that this must be still more so in the case of the rather intermediate hybrids. When such hybrids appear in nature, they are probably hardly noticed for that reason. Only HENKING (1929, 1931) has mentioned the occurrence of such hybrids in the German River Persante and given a description of them. As he points out at the same time, that artificial hybridization between Salmon and Trout often occurred at the German Salmon hatcheries, it is not however certain that the grown-up hybrids described occurred in nature. It should be remembered in this connection, that the two species mostly have different times of breeding, the Sea trout earlier in the autumn and the Salmon later on. Yet the males use to have milt for a rather long time. Mention should also be made that BAUMANN (1954) could not prove the occurrence of such hybrids in the Rivers Rhine and Mosel.

More dissimilar from the parents than the Salmon×Sea trout hybrids are the Salmon×Brown trout hybrids. Even if such hybridization is clearly possible, it is not probable on account of the two species' distribution that any such natural hybridization takes place. The typical form of Brown trout is more unusual at least in Sweden in the waters, where the Salmon occurs, and it usually spawns earlier in the autumn than the Salmon.

The hybrids, which differ most from the parents and which ought therefore to be very easily observed, are the Trout×Char and the Trout×Brook trout hybrids. These are the Zebra (Leopard) fish, or in German die Tigerforelle. Natural hybridization between these species, however, probably occurs very seldom. The Trout and the Char mostly have different breeding places, the former in streams, the latter in lakes. Brook trout seldom occur in our country in the same water as the Trout. If at any place these two species are to be found and they should spawn at the same time, hybridization is of course not impossible, as their breeding places and habits are similar. The great losses as early as the egg and alevin stages make it probable, however, that the result of such a hybridization would scarcely be noticeable. If it should occur often, for example in North America, where in many places both Brown trout and Brook trout are common in the same waters, such hybrids, being easily recognizable on account of their very noticeably dissimilar colour marking, should have been observed and described in the lite-

rature. As has been mentioned above, HOFER (1909) states that such hybrids have been caught in certain German trout waters, where Brook trout had been released. In these cases, though, it is not out of the question that they were artificial hybrids.

Finally as far as hybridization in nature between Char and Brook trout is concerned, it is hardly probable that this generally occurs. The Brook trout is a typical river fish, even if it has been successfully released in a number of small lakes. The Char, on the other hand, is confined to lakes in the majority of cases at least. The one species, therefore, usually spawns in streams the other in lakes. Even in the cases where the Char migrate into running water for spawning, this takes place in more sluggish waters than those usually selected by the Brook trout. Specimens which are said to be intermediate, however, are recorded from some Swedish char lakes into which brook trout were introduced.

VI. **Summary**

1. Artificial hybridization has been carried out with the following species and forms of the Salmon family, namely Salmon, Sea trout, Brown trout f. *lacustris,* Brown trout f. *fario,* Char and Brook trout.

2. In such hybridization the mortality in the eggs and alevins is greater than with intraspecific fertilization. This can be explained by poor fertilization on account of the sexual products not being fully ripe at the same time, or by mechanical impediments to the penetration of the sperm into the eggs, but chiefly by disturbances in the chromosome balance.

3. The mortality due to disturbance of chromosome balance is less the closer the two species used for crossing are to one another systematically. It is thus least in the Char×Brook trout hybrids, median in the Salmon×Trout hybrids and greatest in the Trout×Char and Trout×Brook trout hybrids.

4. In general hybridization is independent of which species is the female fish. If the female fish is very small in relation to the male fish, however, hybridization is generally less successful in the one direction than in the other for the above-mentioned mechanical reasons.

5. The hybrids produced show greater mortality at later stages than the parents. This does not prevent surviving specimens from being able to attain as great an age as the parents.

6. The hybrids have a good rate of growth, mostly intermediate between the parents but often similar to or better than the parent displaying the best rate of growth.

7. The appearance of the hybrids has varied in the same experiment. In certain specimens the type has been intermediate, others have displayed characteristics from one or other of the parents. The Trout×Char and Trout ×Brook trout hybrids have, however, had a very homogeneous colour

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marking consisting of a more or less marked light vermiculation on a dark ground in both the crosses in all the experiments. These hybrids thus differ very noticeably from the parents, while the Salmon×Trout hybrids and the Char×Brook trout hybrids are more reminiscent of the parents.

8. The Salmon×Sea trout and reverse hybrids have undertaken long migrations like the Salmon on being released in the Sea. The Char×Brook trout and reverse hybrids have been hardier and easier to rear in ponds than the Char, and in addition have had a longer term of life than the Brook trout.

9. In all the series of hybrids a greater or smaller number of specimens has become sexually mature. The capacity to form eggs and milt capable of fertilization has, however, been in the same proportion as the mortality in the first stages. It has thus been greater the closer the crossed species were to one another systematically. In the Trout×Char and Trout×Brook trout hybrids no ripe spawn or milt could be produced at all. Intercrossing and backcrossing have only succeeded in the hybrids Char×Brook trout, but mortality in these F 2 hybrids has been greater than in the F 1 ones.

10. The majority of the hybrids have no great value from practical points of view. They can, however, be used for certain experiments in connection with Salmon hatching and rearing (Sea trout×Salmon hybrids). They can also be of some interest as curiosities for transplanting and rearing in ponds (Trout×Char and Trout×Brook trout hybrids).

Only the Char×Brook trout hybrids display such a low rate of mortality and in addition such good characteristics, that they can be recommended for rearing in ponds and releasing in lakes. These hybrids are also the only ones, which owing to their survival rate can be used for testing the value of fish culture.

11. In nature the chances for hybridization between species of the Salmon family are for several reasons probably very small, but the opposite is the case in species of the Cyprinid family and several other freshwater fishes.

VII. References

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Pl. I.
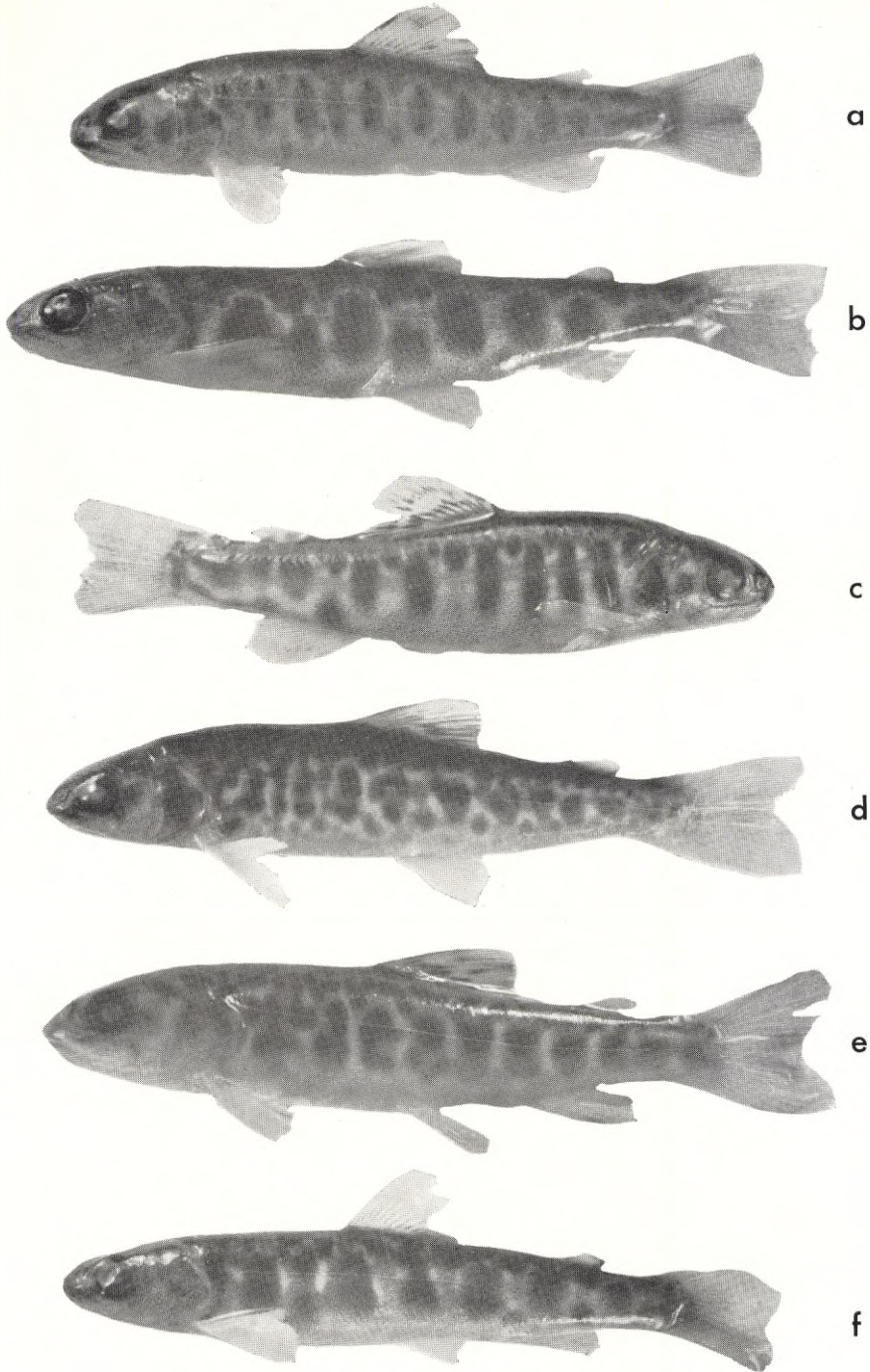
a. Browntrout 6 cm, b. Char 6,5 cm, c. Brooktrout 6 cm, d. Browntrout×Char 7 cm,
e. Browntrout×Brooktrout 7 cm, f. Char×Brooktrout 7 cm. All one summer old.

Pl. II.

a and b. Char×Trout, 2 years old, 17 and 18 cm, different kind of vermiculation, c. Char×
Trout, 4 years old, from a lake, 30 cm, d. Trout×Brooktrout, 10 years old, 46 cm,
e. Char×Brooktrout, 2 years old, 16 cm.

Pl. III.
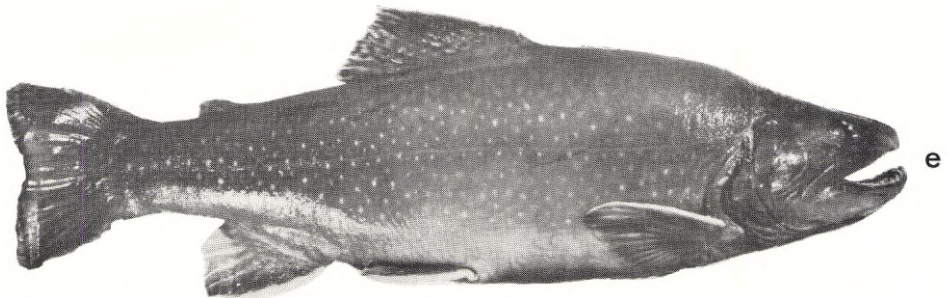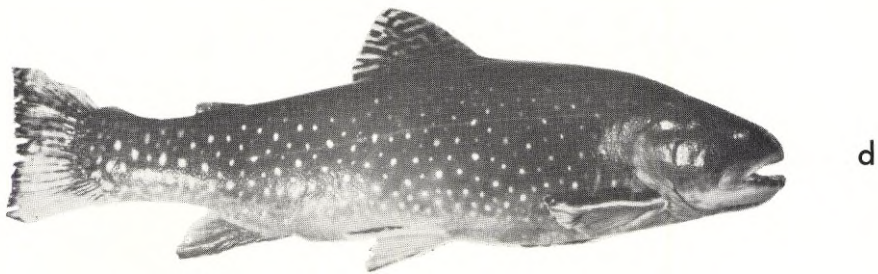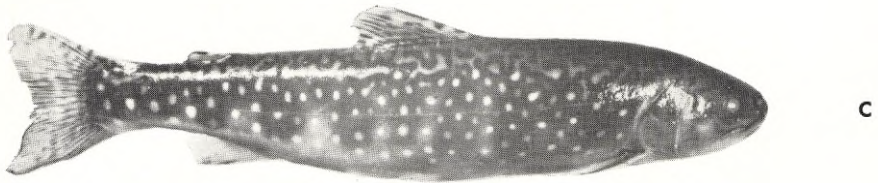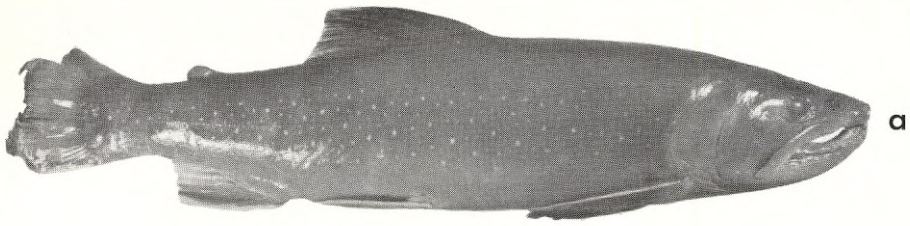
a. Char×Brooktrout, 9 years old, 48 cm, b. and c. Char×Brooktrout, F 2-generation, 2 years old, 17 cm, different pattern of spots and vermiculation, d and e. (Char×Brooktrout) × Brooktrout, 5 years old ♀, 35 cm and ♂ 39 cm.

Tagging of Salmon Smolts in the River Lagan

By Börje Carlin.

Introduction

The River Lagan, which at one time was one of the best salmon rivers in Sweden, has no longer any possibilities for natural propagation of salmon because the river is utilized for hydro-electric purposes. A very limited spawning may, possibly, still take place in the small tributary Smedjeån but reports on this matter are conflicting. To compensate for the loss of the facilities for natural spawning a hatchery was started at Laholm. For several years salmon fry and fingerlings were released with apparently little or no effect. In the last few years salmon have been reared up to the smolt stage before release (MARTINELL 1952). A large number of smolts have been tagged, primarily to try and find if it was possible and economically sound, by the methods adopted at Laholm, to maintain by culture alone a salmon population in a river lacking facilities for natural reproduction.

Method of Tagging

Tagging salmon smolts presents special difficulties on account of the considerable difference in the size of fish between tagging and recapture. Amongst other things the requirements for such tags are as follows: The tag should be capable of being fastened to a small fish without unduly restricting its freedom of movement or causing it other inconvience. The tag must be such as to remain in place for several years without being destroyed or falling off. It must not impede the growth of the salmon or its individual organs (i.e. the fins to which the tag is fastened etc.). It must be readily observed when the fish is caught and should, in addition to a number, bear a message to the fisherman indicating the address to which the tag should be returned. It has not been possible to meet these desirata entirely, but after tests with different ways of tagging, especially different ways of fastening the tag on to the fish, the following method was chosen, which seems to have given better results than obtained previously.

The tag consists of a piece of cardboard coated with celluloid, with a number on one side, the other having a message to the fisherman giving details of the particulars required and the address to which it should be returned. The tag is attached by means of a movable hinge to a wire, both ends of which are separately inserted into the body of the fish immediately under the dorsal fin at a distance of about 6 mm from one another. These ends are twisted together on the opposite side. Thus the wire forms a loop in the body of the fish enclosing one or more interneural bones. In the first experiments the loop was made quite long, about 20 mm, so that the tag would not be so easily grown over as the fish grows. Later on this was changed, so that the loop tied in the body of the fish was made as short and tight as possible, and a piece of wire was inserted, which articulates both with the tag and with the attachement in the fish. In this way the wire lies almost motionless in the body, which diminishes the risk of damage, while the tag readily adjusts itself so as to offer the least possible resistance to the water. The position of the tag on one side of the fish makes it possible for the interneural bones to be used for anchoring the tag without hampering the growth of the fins.

The fish is anesthetized during tagging by using a 2 % solution of ethyl urethane. Two hypodermic needles soldered together are used to facilitate penetration of the wire through the body of the fish.

The wire normally used is soft annealed stainless steel wire of a cheap standard quality (Sandviken 2R2) with a diameter of 0.3 mm. On a few occasions silver wire or monofilament nylon have also been tested. Stainless steel wire has not displayed any apparent disadvantages. No corrosion has been found even after a number of years in sea water, nor are there signs of wear in the loops by which the different parts of the tag are joined together. It is possible that the fine wire has caused a number of tags to be lost soon after tagging by the wire having cut its way out between the fin rays. This has been noticed in a few smolts which were tagged in the autumn and kept over the winter in ponds. The rapid growth of the young salmon when they reach the sea probably very soon lessens the risk of losses of this kind. Silver wire, which had a diameter of 0.5 mm, has given fewer recaptures than the stainless steel, apparently because the wire becomes brittle and breaks. The differences are, however, not great. In one tagging of sea trout smolts in the spring of 1951, on the other hand, silver wire gave considerably poorer results, so that the recaptures of fish tagged with silver wire ceased after a time, whereas recaptures of fish tagged with stainless steel wire continued (Table 1). In this case a heavy growth of red algae and *Mytilus* occurred on the tags, which perhaps implies a heavier load than the silver wire was able to carry. Such a growth does not occur on the salmon tags, and it is probably connected with the fact that trout, unlike salmon, remain near the coast.

Table 1. Recaptures of sea trout, tagged as smolts in the Lagan in the spring of 1951, distributed according to the different materials used for attaching the tags.

Time of recapture	Number recaptured			Percent recaptured		
	Stainless steel	Silver	Nylon	Stainless steel	Silver	Nylon
1951 April—May	18	18	2	3.2	5.1	1.1
June—July	28	12	1	5.0	3.4	2.1
Aug.—Sept.	17	7	—	3.0	2.0	—
Oct.—Dec.	19	1	—	3.3	0.3	—
1952	13	2	—	2.3	0.6	—
1953	4	—	—	0.7	—	—
Sum	99	40	3	17.5	11.2	3.2
Number tagged	566	355	94			

Only to a very limited extent has monofilament nylon been tested, and the percentage of recapture has not been higher than with stainless steel. The nylon was sealed by both the ends being threaded into a tiny spiral of silver wire, which then was pinched flat by a pair of pliers. The sealing was satisfactory, but the nylon caused a greater amount of damage than the metal wire, probably because it is elastic and moves more in the body. Moreover nylon soon wears out where the metal wire rubs against it.

Fish seem to suffer relatively little discomfort from the tag. The wounds where the wire penetrates the body have been very slight, and as a rule they have become entirely healed by the time the fish was recaptured. The tags have a slightly greater specific gravity than water, but the extra weight is negligible so that the mechanical strain on the fish is mainly caused by the resistance of the tag in the water as the fish moves. This is obvious as the tag lies almost straight back when the tagged fish swims even at a moderate speed. It therefore seems more essential to reduce resistance by making the tag small and easily moved in relation to the anchorage rather than to regulate its specific gravity to that of sea water.

Regarding the colour of the tags there are two quite irreconcilable requirements. On one hand the tag should be as conspicuous as possible to the fisherman, so that it is easily seen on capture, but on the other hand it should not attract to much attention of predators. For a fish such as the salmon, which after being caught is treated individually, it seems to be of less importance that the tag should be conspicuous just at the time of the capture than is the case, for example, with herrings. Only a small number of recaptures have been reported from fishmongers or consumers so that it seems likely that the present tag is readily observed by fishermen. On the other hand several tagged smolts have been found shortly after the release in the stomachs of pike in the river. At first white tags were used, but subsequently the tags were made green or blue-green so as to be less conspicuous to predators.

Many tagged smolts have been entangled by the tags in nets of such a mesh that untagged smolts would have passed through them without being caught. Losses from this cause have not been very great, and they have provided some interesting information about the migration of the smolts during the first few weeks in the sea.

In some tagging experiments in other parts of Sweden sometimes a considerable number of captures have not been reported because they were made either by poachers or in the close season. This source of error seems, however, to be of very slight importance in the taggings in the river Lagan, as the fishing on the coast is free to all and the main fishing season is already over before the close season begins. In addition the facilities for salmon fishing in the river are very limited. But it is apparently not unusual for fishermen to neglect to report recaptures owing to lack of enterprize or unwillingness to make the size of their catches known. Especially during the year 1955 this tendency was evident.

The proportion of fish reported is, of course, less than the catches of untagged fish would be up to a comparable stage. Errors arising from this cannot be eliminated entirely by means of improvements in the technique of tagging or the organisation of the tagging experiments, and they have to be taken into consideration when using the material obtained. Apart from recaptures immediately after tagging it is improbable that there are other factors which result in too high a proportion of recaptures. Recaptures immediately after tagging have, however, not been included in the figures for percentage of recaptures in the following discussions.

Material

The salmon smolts have been reared in earthen ponds at the hatchery at Laholm. The ponds have been densely stocked, so that the available natural food played a minor role, at least from a quantitative point of view. The major part of the diet consisted of food brought from the outside, such as liver, fish, and blood. The condition on release has generally been good, although some of the tagged fish exhibited reduced dorsal fins or shortened gill-covers, which defects were apparently caused by deficiencies in diet.

The salmon at Laholm usually reaches smolt size after two years' rearing. They have on the whole been larger and have had a colouring as if further advanced in metamorphosis than the natural smolts leaving neighbouring rivers.

Release

In the majority of cases the smolts have been released into the river Lagan at the hatchery, situated about 10 km from the sea. The river flows smoothly

and without any rapids between Laholm and the sea; only this part of the river is still accessible to salmon. It is not influenced by the very slight tidal movements on this coast. The smolts have been released from the middle to the end of April, which corresponds to the time when the smolts leave the rivers in nature in this part of the country. Usually the smolts have been tagged immediately before release in the spring, but in some cases they have been tagged in the autumn and either kept in a pond communicating with the river by a fish-pass, so that they could go out by themselves in the spring, or kept in ponds that were emptied of fish in the following spring, so that the tagged fish could be examined before release.

On one occasion smolts were tagged and released in the autumn. Some smolts were also released directly in the sea.

Migrations

Immediately after being released in the spring some smolts were caught in the river or found in the stomachs of pike captured in the river. A few smolts have also been taken in stake-nets on the coast near the river mouth. These recaptures have with few exceptions been limited to a short time after release. The smolts thus seems to leave the river and the coast quickly, the majority within two weeks. That the salmon really leaves the coast, so that the cessation of catches after a short time does not depend on changes in the fishing effort, is apparent from the fact that tagged sea trout have been caught after salmon smolts tagged at the same time have ceased to appear in the catches (see Table 1).

No recaptures of salmon smolts have been made on the Swedish coast at any great distance from the river mouth. On the other hand several have been caught on the east coast of Jutland about 2—3 weeks after having been released. The salmon then proceeds to the north past Skagen out into the Skagerrak and then turns towards the west. A great number has been caught in mackerel-nets in the Skagerrak between 2 and 4 weeks after release. After that the tagged salmon are out of sight for about a year. The recaptures of outward bound salmon are shown in the map Fig. 1.

The salmon of the Swedish west coast is not, as the Baltic salmon, subject to fishing in the open sea. For this reason no recaptures have been made on the feeding grounds, and we have no information about where they are situated. Some idea of this can be had, however, from two salmon recaptured in the pre-grilse stage (Fig. 3). One of these was tagged on April 21st 1951 and was caught by a Russian trawler on September 26th the same year in lat. 68°30′ N, long 3°50′ E. It had grown from 16.5 to 35 cm. The other was tagged on April 14th 1953 and was recaptured on August 12th in Steinlands-fjord, northern Norway (lat. 68°50′). It had grown from 15 to 30 cm. A few
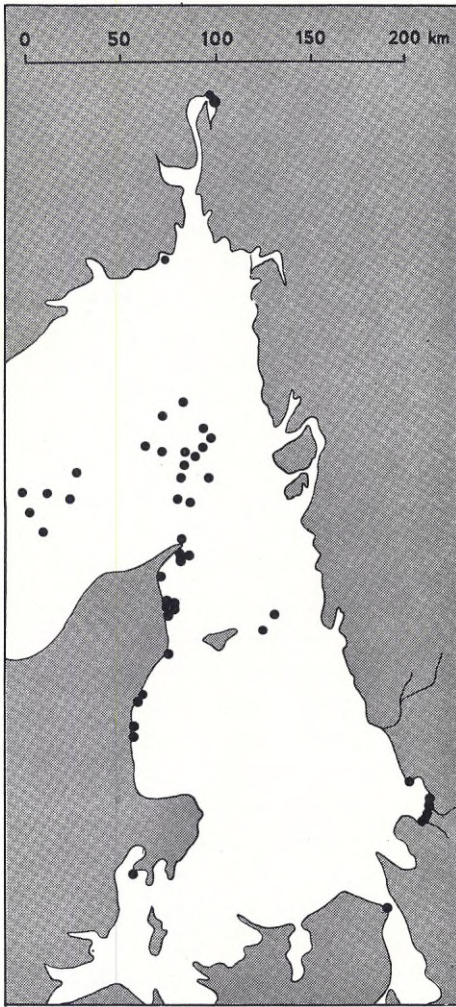
Fig. 1.

Fig. 2.

Fig. 1. Map showing recaptures of outward bound salmon during the first few weeks after tagging.
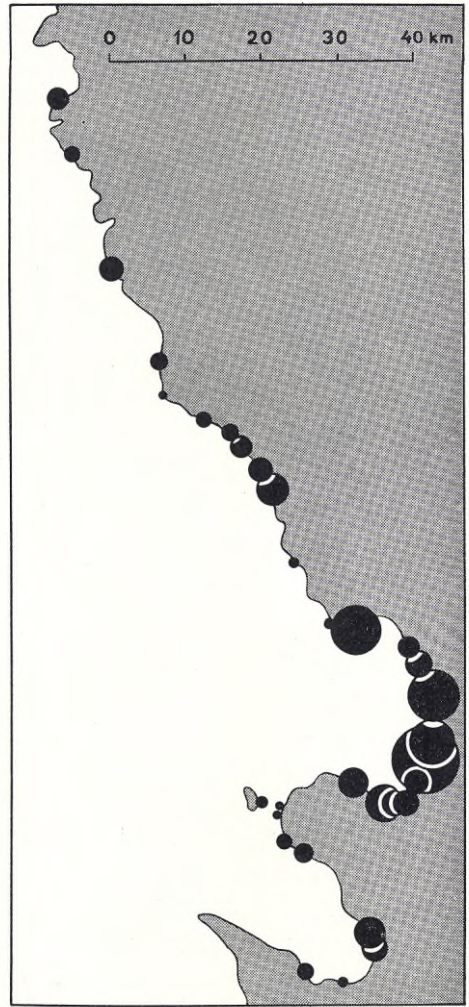
Fig. 2. Recaptures of adult salmon on the Swedish coast. The area of the dots is proportional to the number of salmon caught at the different places.

post-smolts have also been captured in and by the Oslo fjord, namely two in July the same year they were released and one in May the following year. They had grown very little and seem to have been specimens that had happened to come off the usual course.

The two catches of pre-grilse mentioned above are also interesting because, apart from the Baltic area, very few catches of salmon of a size between smolt and grilse are known at all (PYEFINCH 1952, VIBERT 1953, p. 14).

Fig. 3. Map showing recaptures of salmon in the pre-grilse stage (✕) and as adults (dots).

A number of recaptures have been made on the Norwegian coast, all in the outer archipelago. This indicates that the salmon returning from the feeding grounds somewhere out in the North Atlantic pass, at least in part, along the Norwegian coast. The distribution of the catches also seems to indicate that the feeding grounds are situated quite far north. The most northern recapture of returning salmon was made in lat. 64°45′ N, but the majority of recaptures falls between 62° and 60°. A considerable part of all the recaptures during the year 1952 was made in Norway, but the recaptures there were fewer in the following years, as may be seen in Table 2.

The changes in the percentage of recaptures in Norway in the different

Table 2. Recaptures on the coast of Norway.

Recaptured in the year	1952	1953	1954	1955
Total number recaptured	37	260	215	264
Number recaptured in Norway	16	3	9	16
Percent recaptured in Norway	46.3	1.1	4.2	6.1

years may possibly be explained by the fact that even if the returning salmon passes along the Norwegian coast, they normally do so at so great a distance, that only under certain wind and current conditions are they driven so near land that they get into the comparatively narrow zone controlled by the fishing-gear. The salmon probably does not go on to the Norwegian coast purposely, otherwise we would except recaptures also inside the island belt. DAHL & SØMME (1937, p. 12) have shown in their tagging experiments that »most of the salmon which have penetrated the island belt and reached the mouths of the fiords are near the end of their migration». Salmon tagged at places further out, on the other hand, have still undertaken long migrations, and several salmon tagged at the Norwegian coast have later been recaptured on the west coast of Sweden and in rivers running into the sea there (DAHL & SØMME 1935, 1936, 1938, 1941).

Recaptures on the Norwegian coast have been made at about the same time as the recaptures on the Swedish coast, and it has not been possible to trace any significant difference in time corresponding to that which the salmon would take to travel from the Norwegian coast to the Swedish coast in the vicinity of the Lagan river. Apart from the paucity of material this may possibly be explained by the fact that the salmon which come in contact with the Norwegian coast are delayed by wandering there, while those which pass further out continue more directly towards their goal. Salmon tagged on the Norwegian coast and recaptured on the Swedish coast have been caught between 15 and 37 days later (ROSÉN 1948, p. 6).

In Skagerrak as well as in northern and western Kattegatt only a few recaptures of returning salmon have been made, and we have therefore little information about the route taken by salmon through this area.

Large numbers of returning salmon have been caught on the west coast of Sweden (see map Fig. 2). The majority of these catches (about 2/3) have been made in the bight of Laholm, into which the river Lagan flows. The distance between the capes marking off this shallow bight to the north and south is approximately 20 km. Along the coast outside this area many salmon also have been recaptured, the majority between Vändelsöfjorden (about 90 km NNW of the mouth of the Lagan) and Skälderviken (just south of the bight of Laholm). Recaptures in the bight of Laholm have been made to a great extent south of the mouth of the Lagan. South of the bight of Laholm several recaptures have also been made.

It seems therefore as if the salmon is not too much dependent on the coast line for its orientation towards its native river at the end of its migration in the sea, and it may be questioned whether the salmon normally follows the coast at all. The returning salmon are taken on a much longer stretch of the coast north of the river than south of it but this may be because the coastline north of the river mouth follows quite close to the shortest route from the Skagerrak to the mouth of the Lagan. The coastline south of the river mouth on the other hand is almost perpendicular to it. It may be mentioned here that the recaptures of salmon tagged as smolts in the river Ätran (about 50 km north of the Lagan) are concentrated to a still greater extent in the area close to the mouth of the home river, and that about as many are caught south as north of the river mouth.

From this it seems as if three different stages can be distinguished in the return migration of the salmon. The first stage is a migration in the sea more or less straight towards the neighbourhood of the river mouth. The second is a wandering at the coast near the home river under the influence of winds and currents, and the third is the migration up in the river after the salmon has sensed its water.

That a salmon can wander at the coast in different directions before it reaches its goal has been shown by DAHL & SØMME (1938 p. 10) amongst others. HUNTSMAN (1952) also finds a »wandering mechanism» in many cases more satisfactory for explaining the migrations of the salmon than a »homing mechanism». It does not seem as if a salmon follows the coast very closely when searching for its native river. If the first attempt to find it is not successful, he goes out in the sea again and may try the next time some distance from the first place. In connection with this it may be mentioned, that the fyke-nets for salmon fishing in the archipelagoes of the northern Gulf of Bothnia very often are arranged so as to catch the fish going seawards from the coast.

The fishing on the southern part of the Swedish west coast is so intensive that the salmon, which have got into the shore zone controlled by the fishing gear, have very little chance of avoiding being caught quickly. In a tagging experiment made by EDMAN (1954) with grilse on the coast between the rivers Lagan and Ätran 71 % of the tagged fish were recaptured, and 90 % of the recaptures was made within 5 days. Fish from the same tagging place migrated in different directions on different occasions, but with one direction dominating for all the fish tagged on the same day.

Grilse are caught on the coast during a relatively short time, usually in the latter half of June and in July. Certain variations occur from year to year so that sometimes grilse are caught in the last days of May, whereas in other years the first grilse are taken at the end of June. The larger salmon on the other hand may begin to arrive in April, that is to say considerably earlier than the grilse, and they are caught on the coast until the beginning of August.

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The close season starts on August 8th, so that no recaptures are reported from the coast after that time. The catches on the last days of the open season are, however, so few, that it seems likely that the greater part of the salmon run has already passed by that time.

Once the salmon has approached the river mouth, it apparently quickly enters the river, which has no estuary or tidal zone. Of the salmon tagged in the Lagan (including those released on the coast) 223 have been recaptured as adults in the Lagan, no fish being caught in any other river.

As the Lagan lacks facilities for natural spawning of salmon, there is no need for a close season for this river. Fishing is therefore continued right up to the spawning time to provide the breeding fish required for the hatchery. During the regular fishing season salmon are also caught for sale. Fishing can, however, be practised successfully only at low waterflows, mainly at night, when the power station at Laholm is not working. This means that fishing is very dependent on the temporary water flow conditions, and no conclusions as to the time of the salmon run in the river can be drawn from the time of the recaptures, and the number of salmon captured in the river in different years varies not only with the size of the salmon run but also with the fishing conditions.

A salmon, which was tagged in the Lagan in April 1953 was recaptured on June 23rd 1955 at Ockle, east of Ardnamurchan Point, on the west coast of Scotland. In this case it seems probable that the salmon went off its course on its return migration from the feeding grounds.

Salmon from the Swedish west coast do not normally migrate into the Baltic. Sometimes, however, salmon occur on the west coast differing somewhat in appearance from the normal, and they are supposed by the fishermen to have grown up in the Baltic. Salmon have occasionally been caught on the west coast, carrying hooks of the type used in the Baltic (ROSÉN 1948, p. 6). Only one of the smolts tagged in the Lagan has been caught in the Baltic. It was released in the Lagan in April 1952 and recaptured in March 1954 in the southeastern Baltic 20′ north of Stilo. The salmon was stated on tagging to be one year old, which may have been an error in a previous sorting, as it had a length of not less than 25 cm. Its size was thus far above the ordinary smolt size, which may have been a reason for behaving on its migration in a way different from the normal.

On the whole very few of the tagged salmon were found even at a short distance south of the bight of Laholm. One was found a short time after the tagging in the stomach of a garfish caught at Helsingør, but it is possible that the garfish had migrated southwards after swallowing the tagged smolt. Some smolts released in the autumn, that is to say in an abnormal time of the year, have migrated southwards to begin with, although only for a short distance (see p. 68).

Table 3. Distribution of recaptures into year-classes (tagging in the autumn and of one-year-old smolts excluded).

Tagged in the year	Number tagged	Number recaptured					Percent			
		Winters in the sea					Winters in the sea			
		0	1	2	3	Sum	0	1	2	3
1951	1253	1	37	24	—	62	1.6	59.7	38.7	—
1952	3228	—	227	74	4	305	—	74.4	24.3	1.2
1953	4335	—	133	60		193	—	68.9	31.1	
1954	5611	—	200				—			

Numbers of Years in the Sea

Only one tagged salmon returned to the Lagan for spawning in the autumn of the year of tagging. This was a small male weighing 0.35 kg, which was caught in October 1951.

Roughly two-thirds of the recaptured salmon were grilse and one-third salmon which had spent two winters in the sea, although the proportions varied slightly from year to year (Table 3). Only four salmon were caught after 3 winters in the sea. In addition one salmon which was recaptured in 1955 without the tag, but with a nylon string, may have been tagged either in the spring of 1951 or in the autumn of 1951 (and released in the spring 1952).

On the whole salmon that have spent more than two winters in the sea are very rare on the Swedish west coast. ROSÉN (1948 p. 4) found by examination of salmon scales from the Lagan (dating from the time this river still had a natural salmon reproduction) that 26 % had spent one winter in the sea, 72 % two winters and only 2 % three winters.

Release of Smolts in the Sea

In the spring of 1952, 623 two-year-old smolts were released at the seashore about 8 km south of the mouth of the Lagan. Amongst the smolts released at the same time in the river, 1461 came from the same pond. The size and size distribution were the same in both cases.

The total percentage of recaptures were almost the same in both cases, namely 10.27 % for those released in the sea and 10.95 % for those released in the river, but the distribution into year classes was somewhat different. Of those released on the coast 6.74 % were recauptured as grilse and 3.53 % as older salmon, whereas 8.97 % of those released in the river were recaptured as grilse and 1.98 % as older salmon.

The mean weight for the recaptured salmon during the first summer was 2.39 kg for salmon released on the coast and 2.31 kg for salmon released in

the river; during the second summer 5.42 kg for salmon released on the coast and 4.90 kg for salmon released in the river.

The distribution in the different fishing areas shows some differences, especially as regards the capture of grilse during 1953. The salmon released on the coast have found their way back to the bight of Laholm satisfactorily, even if the recaptures were a little more dispersed along the Swedish coast outside the bight than for those released in the river. On the other hand they have been recaptured in the river to a lesser extent. During 1954 the differences were less obvious, but still displaying the same tendency.

Thirty of the salmon released in the river and 14 released on the coast were caught in stake-nets on the coast near the river mouth during the summer of 1953, which closely corresponds to the relation between the numbers in the two releases (expected 31—13). At the same time 47 of those released in the river and 6 of those released on the coast were caught in the river Lagan (expected 37—16). A chi-square analysis shows that the probability for such a divergence depending on chanche alone is less than 1 in 100.

From this we get the impression, that it is not entirely the same mechanism which controls the orientation of the salmon towards the coast in the vicinity of the home river and which lead them into the river.

The ponds, in which the salmon were reared, were fed with water from the river Lagan. Inasmuch as the homing instinct is connected with a memory of the nature of the water in the home river (cf. HASLER and WISBY 1951) this condition may be met with also for the smolts which were not released in the river.

Release in the Autumn

In the end of October 1951, 470 smolts were tagged and released in the Lagan. The mean length was 20.1 cm and most of them were very silvery in appearance. Soon after the release three of the smolts were caught in the river and three on the coast outside the river mouth. In May the following year one was caught at Skagen. It had grown only slightly. Two of the tagged fish were caught in 1953 and two in 1954, which means that only 0.85 % were recaptured as adults. On the same occasion 449 smolts from the same pond were tagged and released in the sea one nautical mile off the shore 8 km south of the mouth of the Lagan. Soon after the release eight smolts were caught near the place of release, two further north in the bight of Laholm, two in the bay Skälderviken and one in the Lagan. In April the following year one was caught in the Skälderviken and one in the river Stensån (which flows into the bight of Laholm about 15 km south of the Lagan). One was caught at Frederikshavn (Denmark) in May. None of them had grown appreciably. In June one post-smolt was caught at Oslo, having

grown from 19.5 to 21.5 cm. Two of the salmon released in the sea were caught in 1953 and four in 1954, so that the total percentage of recapture as adult salmon was 1.34.

Thus in both cases the total percentage of recapture was low, and evidently the release of smolts in the autumn is unsuitable. The smolts seem to have less inclination to leave the coast in the autumn. Some smolts have immediately gone out the sea, but on the other hand some of those released in the sea have returned to fresh water again. A number of smolts have gone south along the coast after being released, whereas the smolts released in the spring never do.

These smolts were, however, unusually large, which may have resulted in a behaviour somewhat different from that of smolts of a more normal size.

Release of One-year-old Smolts

In the spring of 1952 a number of the largest one-year-old salmon were sorted out and temporarily put in a rearing-trough to be later returned to the ponds for continued rearing. In the course of only a few days they changed from the parr attire to a very silvery appearance, so it was decided to release them. Thus 1462 specimens were tagged and released into the Lagan. Most of them were between 11 and 15 cm long (mean length 13.0 cm). A few were larger than 15 cm and it is probable that some of the largest belonged to an older year-class left over in the pond on a previous occasion when the ponds were emptied.

The recaptures were few. Only six returned as grilse and one after two winters in the sea. In addition one was recaptured in the south-eastern Baltic, as mentioned above. All the recaptured salmon were among those over 14 cm when tagged.

At the same time, that is in the spring of 1952, 2300 one-year-old smolts reared in troughs were tagged and released in the river Örekilsälven and outside its mouth on the northern part of the Swedish west coast. They too had become very silvery in appearance within the course of a few days. With the exception of a few recaptures immediately after the tagging, not a single recapture was reported.

A possible explanation for the few recaptures could be that the smolts, in spite of the obvious outer signs, had not in all respects undergone the metamorphosis into the smolt stage, which makes them capable of enduring the change from fresh-water to sea-water. It should be observed, however, that even among the two-year-old smolts from Laholm very few recaptures have been obtained of such fish that were under 14 cm on being released (see below). This is all the more remarkable, as the smolts, which have been trapped and tagged in the adjacent river Ätran and have yielded a high

Distribution in length classes at tagging.
o o--o--o--o o Percent recaptured as grilse.
● ●—●—●—● ● Percent recaptured, total.
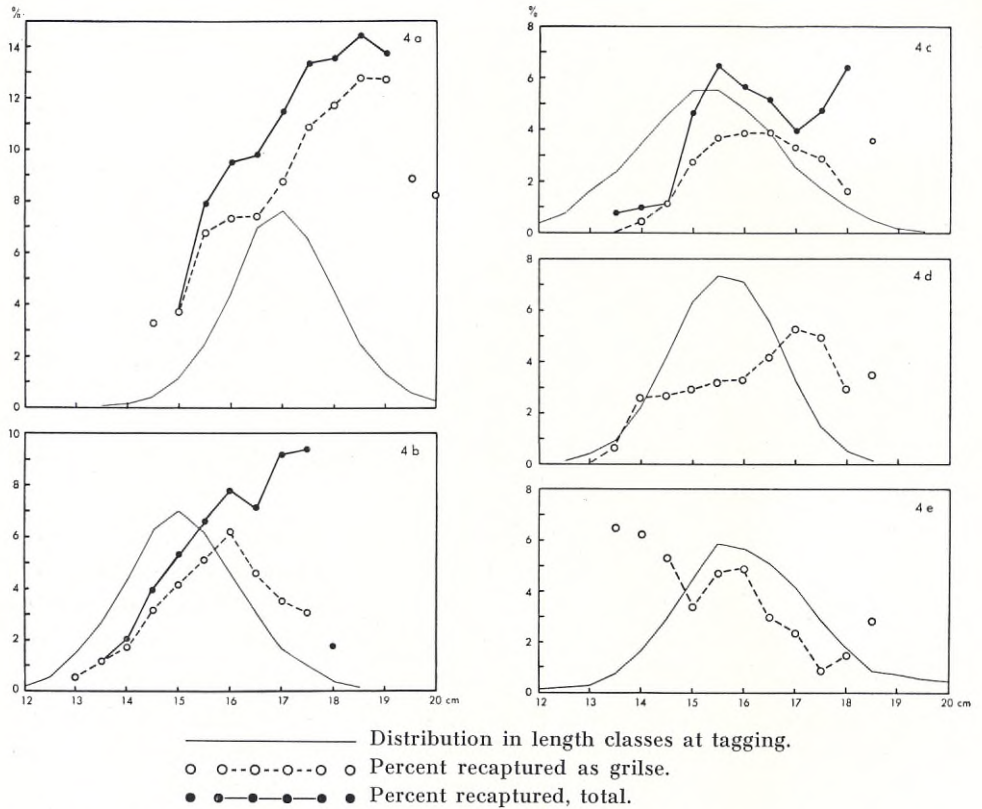
Fig. 4 a—e. Diagrams showing the relation between the percentage of recaptures and the length of the smolts at tagging. — 4 a: Smolts from pond no. 2, tagged in 1952. — 4 b: Smolts from pond no. 2, tagged in 1953. — 4 c: Smolts from pond no. 1, tagged in 1953. — 4 d: Smolts from pond no. 2, tagged in 1954. — 4 e: Smolts tagged in the autumn 1953, released in the spring of 1954.

percentage of recaptures are not much larger on migration (mean length about 13 cm) and considerably less silvery in appearance than the one-year-old smolts in the above-mentioned experiments.

The Size of the Smolts

Smolts of different sizes in the same tagging experiment have given different percentage of recaptures. Some examples of this are shown in the diagrams fig. 4. On the whole the percentage of recaptures increases with increasing size of the smolts, and this increase can be quite considerable. Evidently the chance of survival is to a great extent influenced by the smolt size. A similar thing was found by FOERSTER (1954) who has shown that

Table 4. Correlation between weight at recapture and length at tagging.
(Smolts from pond no. 2 at Laholm.)

	Tagged in the year	Number recaptured with stated weight	Correlation coefficient r	Confidence level P	Regression coefficient b	Mean weight kg	Mean length	
							of all tagged cm	of the recaptured cm
Recaptured after one winter in the sea	1952	173	0.3125	< 0.001	0.198	2.33	17.13	17.27
	1953	98	0.2113	< 0.05	0.127	2.10	15.18	15.43
	1954	105	0.2031	< 0.05	0.096	2.17	15.61	15.95
Recaptured after two winters in the sea	1952	47	0.4828	< 0.001	0.578	5.10	17.13	17.18
	1953	39	0.2896	> 0.2	0.111	4.67	15.18	15.63

there is a very conspicuous increase in the return of spawners of sockeye salmon with increasing smolt size.

In some cases the percentage of recaptures has been lower for the largest smolts, and also in other respects there are exceptions from the rule. The present material, however, is not suited for a more detailed study of this matter as the fish have been sorted every spring and autumn whilst they were being reared.

The weight on recapture has in some cases, when the number of recaptured salmon with stated weight has been sufficient for an analysis, shown a positive correlation to the length of the smolts at tagging. This is shown in table 4, where the regression coefficient denotes the average increase in weight in kilogrammes for every centimeter increase in length at tagging.

Defects

At the tagging in the spring of 1953 it was noted that 393 of 4050 tagged smolts had shortened gill-covers on one or both sides. Four of these salmon were later recaptured, corresponding to 1.02 % of the number released, while 180 specimen or 4.92 % of the remainder were recaptured. Smolts with shortened gill-covers (1174 in number) tagged in 1954 gave 27 recaptured grilse or 2.30 %, while 138 or 3.52 % were recaptured from 3923 undamaged smolts. The higher percentage of defective smolts in the latter case and the smaller difference in percentage of recaptures may have been due to the fact that even very slight defects were recorded.

Shortened gill-covers, which quite often appear in artificially reared fish, seem to be of little disadvantage to the fish while being reared. It does not seem to cause mortality or reduce the growth appreciably. The result of the tagging experiments shows, however, that the defect is rather serious.

Percentage of Recaptures

A summary of all the taggings and recaptures are given in table 5. The figures are not strictly comparable, as there have been differences in size distribution and probably in other conditions too between fish released in different years and between fish from different ponds released in the same year. In three of the experiments the figures have been exceptionally low, namely when one-year-old smolts were released and in two cases when smolts were released in the autumn.

For comparison some figures from tagging of fish grown up in adjacent rivers (from investigations not yet published) may be mentioned. In the river Stensån 98 smolts were caught by electric fishing in the autumn of 1951 and tagged. Seventeen of them have been recaptured as adults, giving a recovery of 17.3 %. In the spring of 1952, 1044 seaward migrating smolts were caught and tagged in a trap in the river Högvadsån, a tributary to the river Ätran, 90 being recaptured, or 8.6 %. In a corresponding experiment in 1953, 98 were recaptured out of 626 tagged fish, or 15.7 %.

The tagging experiments in the river Lagan have thus not given quite so high percentages of recaptures as with the tagging of naturally grown smolts in adjacent rivers, but closer comparisons ought not to be made, as amongst other things the fishing conditions in the rivers are very different. It may, however, be concluded from these experiments, that the recoveries are sufficiently numerous to encourage us to continue artificial propagation of salmon in the form of rearing up to the smolt stage.

Summary

About 17,000 salmon smolts from the salmon hatchery at Laholm were tagged before release into the River Lagan. In different experiments the proportion of recaptures ranged from 5 to 10 % which indicates that artificial propagation of salmon in this way may be sound from the biological and economical points of view.

The recaptures make it possible to follow part of the migrations of the salmon, firstly on their outward journey as far as to the middle of the Skagerrak, and on the return journey along the coast of Norway and Sweden. No recaptures were, however, made at the main feeding grounds, the locations of which are not yet known. Of the salmon recaptured as adults 353 out of 778 were caught on the coast in the immediate vicinity of the mouth of the Lagan and 223 in the River Lagan itself. No fish were retaken in any other river.

The majority of the recaptured tagged salmon were retaken after one

Table 5. Summary of all tagging experiments and recaptures.

Tagged in	From pond no.	Number tagged	Mean length cm	Number recaptured — after one winter in the sea					Number recaptured — after two winters in the sea							After three winters in the sea (Swedish coast)	Total	Percent recaptured — After one winter in the sea	After two winters in the sea	After three winters in the sea	Total
				Norway	Denmark	Swedish coast	R. Lagan	Total	Baltic	Scotland	Norway	Denmark	Swedish coast	R. Lagan	Total						
1951 spring	(mixed)	1253	16.3	16	—	19	3	38	—	—	2	1	17	4	24	—	62	3.03	1.91	—	4.94
1951 autumn (river)	4	470	20.1	—	—	1	1	2	—	—	—	—	1	1	2	—	4	0.43	0.43	—	0.85
1951 autumn (coast)	4	449	20.0	—	—	2	—	2	—	—	—	—	4	—	4	—	6	0.45	0.89	—	1.34
1952 spring	1[1]	73	17.3	—	—	3	—	3	—	—	—	—	1	—	1	—	4	4.11	1.37	—	5.48
1952 spring	2[2]	335	17.1	—	—	10	5	15	—	—	—	—	5	3	8	1	24	4.48	2.39	0.30	7.16
1952 spring	1	38	17.1	—	—	1	—	1	—	—	—	—	1	—	1	—	2	2.63	2.63	—	5.26
1952 spring	2	1461	17.1	—	4	80	47	131	—	—	—	—	20	7	27	2	160	8.97	1.85	0.14	10.95
1952 spring	3	698	16.6	1	—	24	10	35	—	—	—	1	10	4	15	1	51	5.01	2.15	0.14	7.31
1952 spring	4.5[3]	1462	13.0	—	—	4	2	6	1	—	—	—	—	1	2	—	8	0.41	0.13	—	0.54
1952 spring (coast)	2	623	17.2	—	—	36	6	42	—	—	—	—	18	4	22	—	64	6.74	3.53	—	10.27
1953 spring	1[1]	60	15.3	—	—	—	1	1	—	—	—	—	1	1	2	—	3	1.67	3.33	—	5.00
1953 spring	1	1175	15.2	2	—	14	11	27	—	—	—	—	13	3	16	—	43	2.30	1.36	—	3.66
1953 spring	2	2875	14.7	7	—	44	50	101	—	1	1	—	20	18	40	—	141	3.51	1.39	—	4.90
1953 spring	trough	225		—	—	2	2	4	—	—	—	—	—	2	2	—	6	1.78	0.89	—	2.67
1954 spring	1[1]	795	16.2	3	—	17	8	28	—	—	—	—	—	—	—	—		3.52			
1954 spring	2[2]	219	16.2	1	1	4	1	7	—	—	—	—	—	—	—	—		3.20			
1954 spring	2	3560	15.6	6	1	92	18	117	—	—	—	—	—	—	—	—		3.29			
1954 spring	3	549	16.1	2	—	14	2	18	—	—	—	—	—	—	—	—		3.28			
1954 spring	4	988	15.4	3	—	19	7	30	—	—	—	—	—	—	—	—		3.04			

[1] Tagged in the previous autumn, not examined in the spring.
[2] Tagged in the previous autumn, released in the spring after being examined.
[3] One-year-old smolts.

winter in the sea, most of the remaining after two winters and only a few after more than two winters in the sea.

Results for smolts liberated directly into the sea were as good as for those released in the river. Autumn liberations resulted in a low percentage of recoveries, as was also the case when one-year old smolts were released. The percentage of recoveries generally increased with a rise in the smolt length. There is a positive correlation between smolt size and size at recapture.

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Observations on the Spawning Behaviour of the Grayling, *Thymallus thymallus* (L.)

By Eric Fabricius and Karl-Jakob Gustafson.

Contents

1. Introduction

According to HECKEL and KNER (1858), the spawning grayling »move in couples to suitable places, where, by means of the caudal fin they dig a hole for the eggs which, after the fertilization, are covered by gravel and small stones». This short description has been cited by several authors (SMITT, 1895, ALM, 1942, and others), but no detailed account of the spawning behaviour of grayling has been published, as far as we know. Apparently one of the reasons for this lack of observational data has been the fact that the grayling is known to be difficult to keep in aquaria. Thus SMOLIAN (1920, p. 102) claims that the grayling »laicht nicht in Gefangenschaft».

The grayling is of importance for the commercial and sport fishing in many lakes and streams of northern Sweden. In many cases the spawning streams of the grayling are subjected to interference by water regulation for the hydroelectric power industry, or by cleaning out of the stream beds to facilitate the timber floating.

As it was felt that it would be desirable to find out what environmental

conditions are necessary for the reproduction of grayling, aquarium experiments as well as field observations on spawning grayling were made in 1954 and 1955. Grayling from Lake Storsjön were used in both the aquarium experiments.

The 1954 experiment was made in the stream tank of the Hölle laboratory. This tank, which is 950 cm long, 190 cm wide and 70 to 130 cm deep, has been described in detail by LINDROTH (1954). During the experiment the depth of water was kept at about 70 cm and the velocity of the current running through the tank was about 0.5 metres per second. As described by LINDROTH (op. cit., p. 114), the tank has a deeper area, adjacent to the observation room, and this area can be separated from the shallow area by a longitudinal wall. We used only this deeper part which has a bottom area of 85×950 cm. Five sections with different bottom material, ranging from fine sand to fairly big stones, were set up. The grayling showed fighting, territorial and courting behaviour, but they did not spawn in this tank.

As we supposed that the fish had in some way been damaged by the long transport from Lake Storsjön to the Hölle laboratory, we decided to build an aquarium at a grayling brook in 1955, and to lift spawning grayling directly from this brook into the tank. A suitable place was found at the Hegledbäcken, which is one of the numerous small brooks into which grayling from Lake Storsjön migrate to spawn in April and May (GUSTAFSON, 1948). From the top of a water fall a wooden chute was built, which transported water into one end of an aquarium. The water then passed through the tank, ran over an overflow sluice at the opposite end of it, and returned to the brook by another chute. The tank was 215 cm long, 57 cm wide and 54 cm deep. A canvas shelter was built over the aquarium, electricity supply was arranged by a long cable from the Fanbyn village, and bulbs for photography were fitted over the tank.

The water temperature in the tank was the same as in the brook. During cold nights it could sink to about 0.5° C, and in sunny days it could rise to about 10° C, or slightly more. The maximal temperature was usually reached at about 3 p.m.

The grayling spawned in this Hegledbäcken tank, but not until the bottom material had been arranged in a particular way, based on field observations made at the natural spawning grounds in the brooks (p. 85). About 100 complete spawning acts were watched in the aquarium. The intense light of the twentytwo 500 watt bulbs over the tank did not disturb the fish, and thus K.-J. Gustafson could make a 16 mm coloured ciné film, showing the whole spawning behaviour of the grayling.

In addition to the aquarium experiments, field observations on territorial behaviour and spawning were made at the Hegledbäcken and Svartbäcken creeks. Polaroid glasses, which eliminated much of the light reflections from the water surface, were found to be very useful in these observations. In
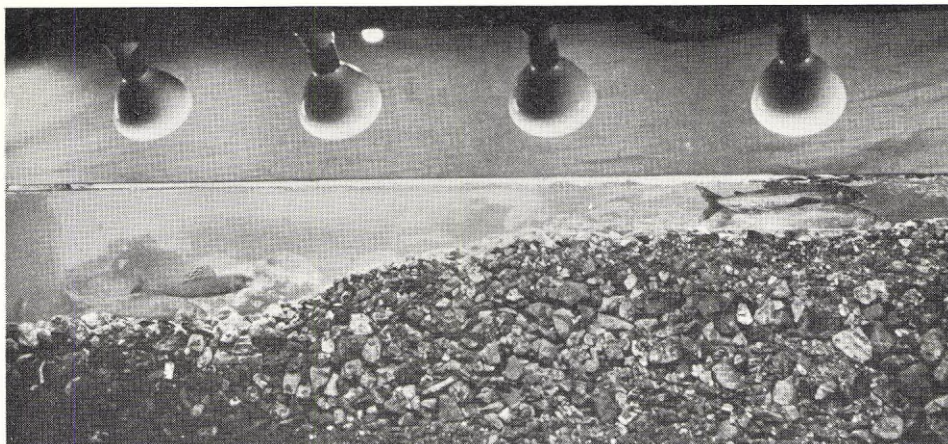
Fig. 1. Two pairs of grayling in the observation tank at the Hegledbäcken creek. Both the females show the posture of readiness. The gallery of caves is visible in the background. The water is flowing through the tank from right to left. Photo: K.-J. GUSTAFSON.

May and June 1955 we watched 15 spawning acts in the Svartbäcken and 5 in the Hegledbäcken. One spawning act and some boundary disputes between territory guarding males were filmed in these streams.

2. **Threatening and Fighting**

In the grayling aggressiveness is common in both sexes and at all times of the year, and it occurs in young immature specimens as well as in adult ones. During the spawning season the frequency of aggressive behaviour is much increased however, particularly in the males.

Outside the breeding season the grayling tend to form schools, and one need not watch such a school for long to see hostile encounters between its members. The school usually maintains its position in the stream, at least for some time, and within the school each fish is hovering at its own station, for example over a stone or tree root on the bottom.

The individual stations are defended as small territories. If one of the grayling approaches another one too closely, the approached fish will respond by erecting its dorsal and pelvic fins. The grayling has a very big dorsal fin and this, as well as the pelvics, has a complicated pattern of brightly coloured spots, while all the other fins are of a uniform dull colour. If the intruder flees, the territory owner often makes a sudden forward dash and bites it in the tail. If the intruder does not flee at the display of the erected fins, the territory owner swims towards it, and a most spectacular act of mutual lateral display follows. The two opponents swim side by side, touching
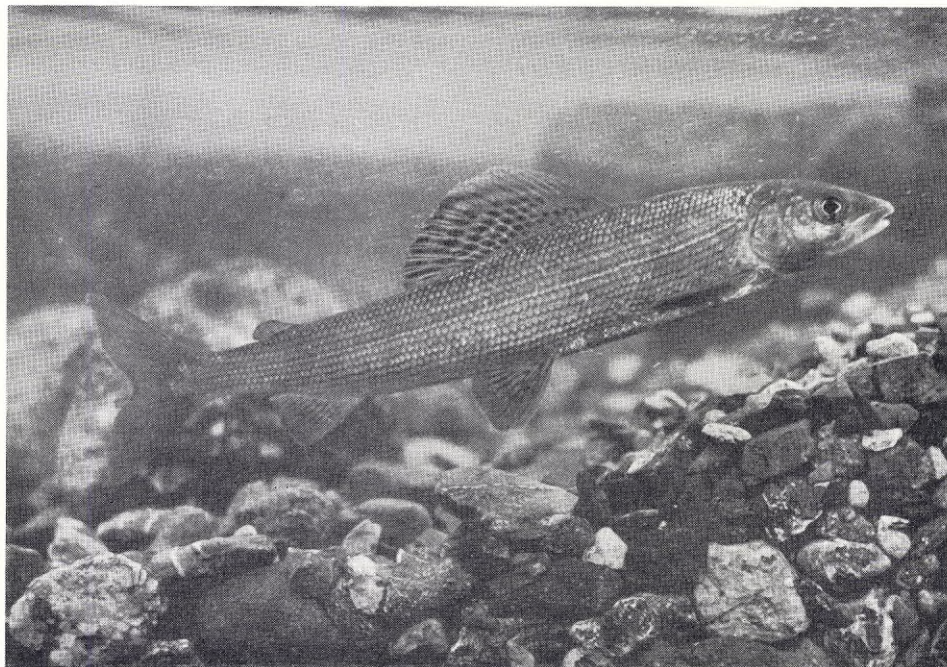
Fig. 2. Male grayling in a normal swimming posture. Photo: K.-J. GUSTAFSON.

each others flanks, erecting their dorsal and pelvic fins to their full extent, and at a high intensity of this act they perform a trembling movement, quite similar to the trembling in the courting of salmon, trout and char. At a high intensity of the mutual lateral display, the grayling also lower the under part of the mouth, displaying the white throat, which on each side has a black spot, visible only when the mouth bottom is lowered. (Fig. 3). The lowering of the under part of the mouth during the lateral display is performed also by young specimens, in which the black spots on the throat are not yet developed. Except in the lateral display, the under part of the mouth is also lowered in yawning. It should be mentioned in passing that yawning in grayling and char does not seem to have any connection with aggressiveness or any other social behaviour patterns. It is often performed spontaneously, for example while a fish is resting and no other fish is visible. BAERENDS and BAERENDS (1951) regard the yawning in cichlids as a »comfort movement» and apparently this is the case in salmonids as well.

During the mutual lateral display the two opponents usually travel forward, often for a distance of several meters. In flowing water they head against the current, pushing themselves against each others flanks. This usually results in a movement obliquely across the stream, because the weaker fish is pushed sidewards. While moving side by side in this way, each of the two fish tries
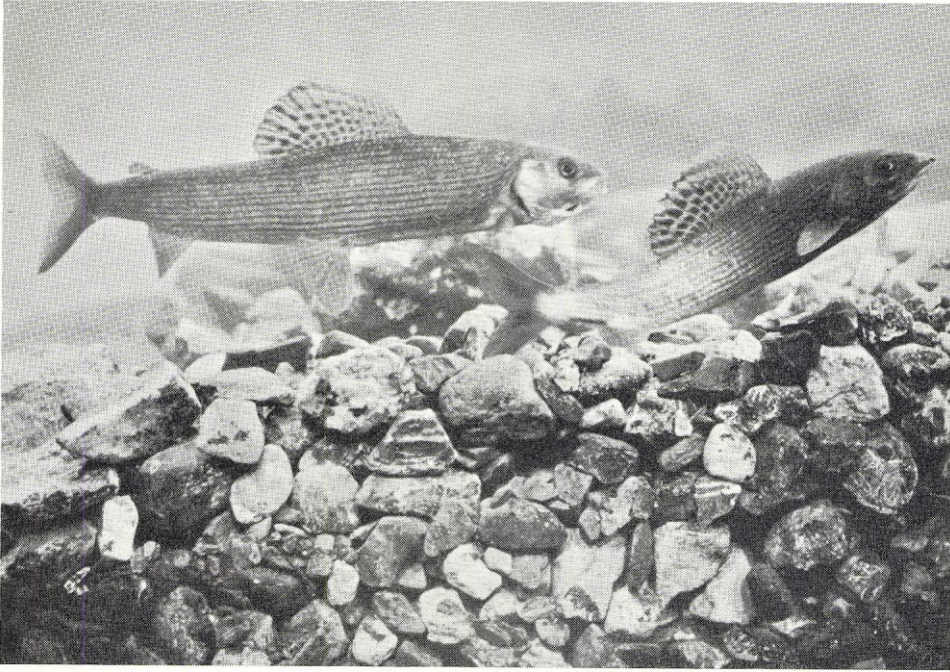
Fig. 3. Two threatening males. The specimen to the left shows the lateral display. The dorsal fin and the pelvics are erected to their fullest extent and the under part of the mouth is lowered, displaying the black patch on the throat. Photo: K.-J. GUSTAFSON.

to swim past the other one, and to turn across the current in front of its nose. If this manoeuvre is successful, the water current carries the rear fish downstream, pushing the opponent away. If the intruder withstands this manoeuvering, the territory owner suddenly turns its head sidewards against the enemy and bites it. Sometimes the attacked fish then makes a counterattack, and a fierce fight follows, in which the two opponents move side by side, biting and pushing each other, and performing vigorous trembling movements. In shallow water such a fight is accompanied by a lot of splashing. During 390 minutes of timed observations of a group of 3 males and 3 females in the Hölle tank, mutual lateral display was observed 283 times between males, 244 times between a male and a female, and 56 times between females. The average length of the acts between males was 7 seconds (1 to 22 sec.), and that of the acts between a male and a female 6 sec. (1 to 20), while the acts of lateral display between females had a mean length of 5 seconds (1 to 15).

Fighting grayling always move side by side, and the biting is just a sudden nipping. We have never seen them showing the characteristic fighting pattern of char and trout, which are often seen gripping hold of each other by the
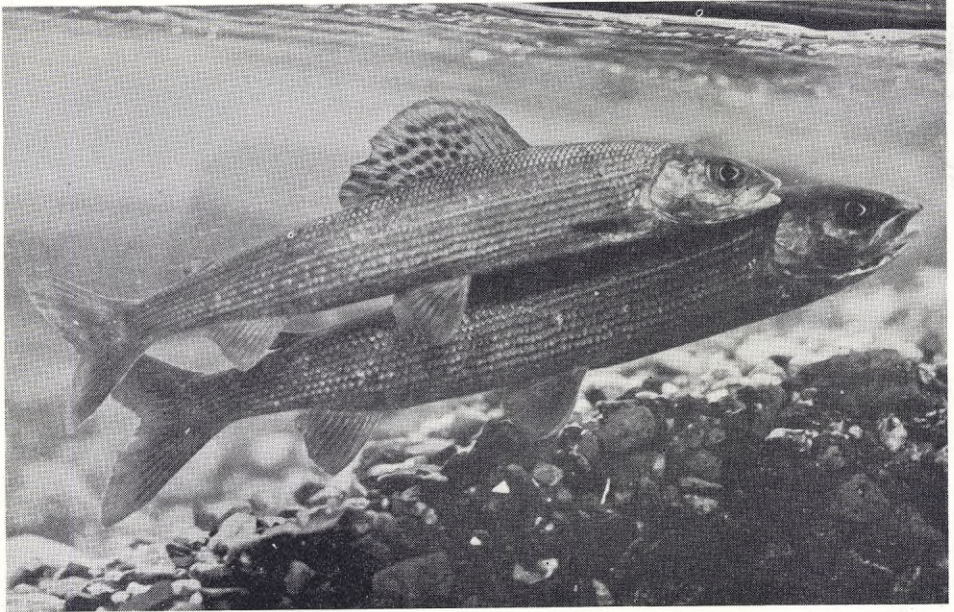
Fig. 4. Two fighting males, swimming side by side. Photo: K.-J. GUSTAFSON.

jaws for a long while, or circling round each other, repeatedly biting each other in the tail (cf FABRICIUS 1953, JONES and BALL 1954, and others).

Most probably the extreme size of the dorsal fin and the bright colouration of this fin and of the pelvics has developed in the grayling in connection with the important role of the lateral display in the fighting behaviour of this species. Fish living in streams tend to head against the current, and this makes it more natural for them to approach each other side by side than to make frontal attacks. In erecting the dorsal fin and the pelvics but no other fins, the grayling resembles the whitefish, *Coregonus*, which erects these fins in its act of »sailing» (FABRICIUS and LINDROTH 1954), a display of unknown function.

The visual stimuli releasing the attack are probably very simple. A male attacked a black photometer that was moved close to the front pane of the Hegledbäcken tank.

3. The Vibrating Display

In this behaviour the fish, hovering in the water, bends the caudal part of its body upwards, so that the tail is lifted, erects its dorsal and pelvic fins to their full extent, and performs vigorous and very swift trembling body movements. The erection of the dorsal and pelvic fins is so spasmodic that these fins often are more or less twisted, as can be seen in fig. 5. The vibrating
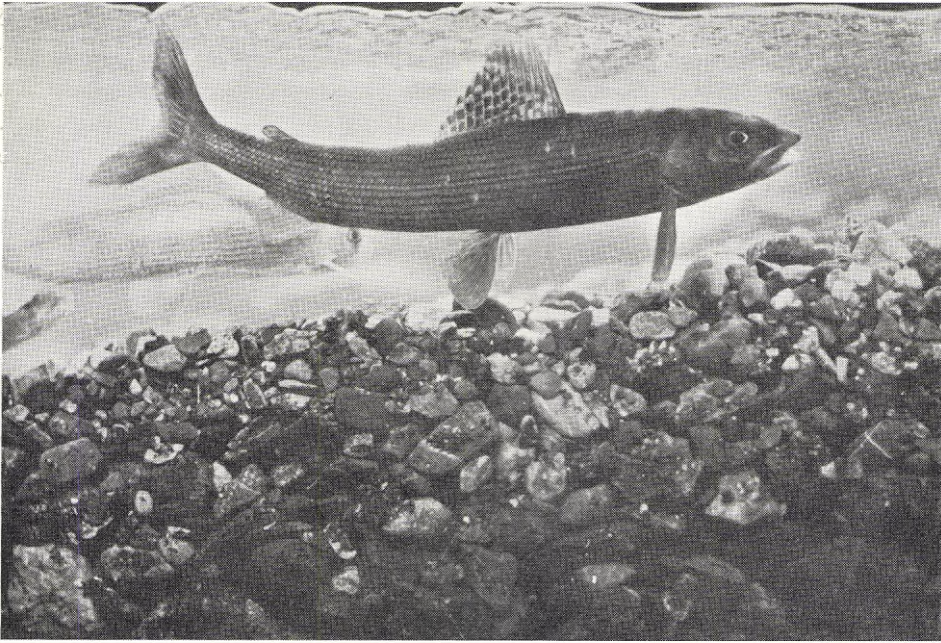
Fig. 5. A male performing the vibrating display. Note the bending of the caudal peduncle and the twisting of the dorsal fin. Photo: K.-J. GUSTAFSON.

display lasts up to 10 seconds on each occasion. During this act the fish often temporarily loses its orientation and is carried backwards by the current.

The vibrating display was observed only in adult specimens, and only during the spawning season. In the Hölle tank, where grayling did not spawn, is was seen approximatively as often in females as in males, but in the Hegledbäcken tank, where spawning occurred and the conditions apparently were more normal, vibrating display was seen about 200 times in males, but only 3 times in females, which indicates that it normally belongs to the male behaviour pattern.

Usually the vibrating display was performed by territory owners shortly after an attack on a trespasser, but it was also very often manifested spontaneously, by males which were for the moment quite alone in their territories. If other fish are present, the vibrating fish does not, as a rule, orientate itself towards them in any way, but on one occasion it was seen that a male approached another male which was resting on the bottom, trembled against his flank in an act of lateral display, and then the intensity of the trembling increased, and the fish adopted the posture of the vibrating display and was carried backwards by the current.

A territory defending male that was watched in the Hegledbäcken tank for

a period of 30 minutes, made 48 attacks on trespassing males and unripe females, courted ripe females 29 times, and performed the vibrating display 10 times. During another 30 minutes period, this same male showed 5 attacks, 22 courting acts, 2 actual spawning acts, and only 3 acts of vibrating display. This seems to indicate that the vibrating display functionally belongs to the aggressive behaviour rather than to courting and mating, but it should be mentioned that we also have seen males performing it immediatly before a spawning act.

Probably the vibrating display has a similar function to the song of many passerine birds and the display postures of, for example, male gallinaceous birds and birds of paradise, i.e. it advertises the presence of the territory owner, frightening rivals and attracting females. It should, however, be emphasized that some of the movements that build up the vibrating display, particularly the very swift trembling and the lifting of the tail, apparently are fixed motor patterns belonging to the mating act, and that the vibrating display looks very much like an incomplete mating act of medium intensity, performed as a »vacuum activity».

4. Territorial Behaviour

On reaching the spawning grounds, the male grayling show a strongly increased aggressiveness. They begin to defend such large territories (up to 16 m² or more) that they lose contact with one another and the schools disperse, and if undisturbed, each male remains in his territory for at least one week. In the spawning streams, several territories often border on each other, forming small colonies.

Some observations on the minimum size of the territories could be made in the tanks. In the big Hölle tank every male defended a territory, even if as many as ten males were kept in the tank. In the Hegledbäcken aquarium, which had a bottom area of 215×57 cm, we at first made an even bottom of gravel and small stones, slightly sloping from the upstream to the downstream end of the tank. As long as the bottom material was arranged in this way, only one male could defend a territory. From April 14th to May 29th we on several occasions released groups of 3 to 4 ripe males and some females into this tank, and these experiments always gave the same result. In the beginning all the males showed aggressive behaviour, and a lot of fighting was seen, but after some hours or some days one of them became dominant and defended the whole tank as his territory, while all the other fish were driven together to the downstream end of the aquarium. On one occasion, however, a second male succeeded in defending a territory, but only in a »halfhearted» way. This male, »B», took its position at the upstream end of the tank, while the dominant male, »A», held its position in the centre

of the aquarium. The B-fish did not defend its territory against the A-fish, which sometimes made excursions into it, but it attacked two females and a third male which now and then swam to the upstream end of the tank, leaving the downstream end, where they were usually driven together by the dominant A-fish. Sometimes the B-fish was carried backwards by the current, into the A-territory, and on these occasions the A-fish attacked it and pushed it to the downstream end of the tank, from where it soon rushed back to the upstream end, into its own territory. The fish had thus established a sort of peck-order in which only the two strongest males defended territories, and the male »A» attacked all the other fish, male »B» attacked all except »A», while the remaining fish were more or less submissive. Actually the situation was even more complicated, because one of the females attacked the other female as well as the third male, but she was never attacked by them. Similar situations very often develop when territory defending species of fish are kept in too small tanks (references in FABRICIUS and GUSTAFSON 1954, p. 63. See also JONES and BALL 1954).

On May 30th the bottom material of the tank was rearranged. A mound of gravel, almost reaching the water surface, was made in the middle of the tank, dividing it into two pools, one upstream and the other one downstream of the bank. The upstream pool was slightly smaller than the downstream one. On May 30th, at 8 a.m., 3 males and 7 females were introduced into the tank. After a series of fights, which lasted about 10 hours, one of the males had established a territory in the upstream and another one in the downstream pool, while the third male had been driven to the downstream end, together with the females. The two successful males defended territories until June 4th, when the experiment was finished. Now and then they penetrated into each others territories and fought violent battles, passing over the top of the bank to do so. The size of the upstream territory was about 40×50 cm, while the downstream territory had an area of about 40×80 cm. The fish defending the upstream territory was considerably larger than the specimen guarding the downstream pool. These experiments, demonstrate that the number of territories can be increased if the bottom material is arranged in such a way that the different males are visually isolated from each other, a fact which is well known in several species of fish (references in FABRICIUS and GUSTAFSON 1954). The róle of visual isolation in determining the size of the territories in the natural spawning streams will be discussed in chapter 8.

In his territory every male has a »station», which usually is situated either behind a stone, a gravel bank, a tree root or a log, or in the »cushion» of comparatively immobile water, formed at the upstream side of such an obstacle. Hovering at his station, the male watches his territory, reacting to any intruder, male or female, by a hostile approach. Males and unripe females are driven away by lateral display and attacks. When the intruder comes

into the territory from the upstream end, the resident male swims towards it, heading against the current, but if he discovers intruders downstream of himself, he often lets the current carry him backwards, tail first, and approaches them in this way.

If no intruders appear, the male now and then leaves his station for a patrol cruise in his territory, or makes an exursion into one of the neighbouring territories. There he is attacked by its owner, which sometimes after a long fight, drives him back into his own territory. The longest fight we watched in the field lasted 24 minutes, and in the Hegledbäcken tank we observed two males figting for 26 minutes when one of them had made a visit into the territory of the other one. It often happens that two fighting males move into the territory of a third male and are attacked by him, and in this way groups of three or more fighting and laterally displaying fish can be temporarily formed.

A male that was watched for 25 minutes in a pool in the Hegledbäcken creek left his station 22 times, of which 8 times were for attacks on trespassing fish, 6 times for patrol cruising in his territory, twice for visits into the nearest territory downstream of his own, and 6 times for visting the territory of his upstream neighbour.

The frequent visiting of neighbouring territories, which gives the impression of an »appetitive behaviour for fighting», is known to occur also in some other species of fish, for example in *Abramis brama* and *Tanichthys albonubes* (FABRICIUS 1951), and we have seen it also in the char, but, according to BAERENDS and BAERENDS (1950) it is rare in cichlids, which usually stop at the boundaries of their territories.

In both the aquarium experiments it was occasionally observed that females could also defend territories, though these were usually smaller than the male territories, and the females did not remain in their territories so long as the males. In the natural streams it was difficult to observe the behaviour of the females, because they usually dwelled under overhanging banks.

Finally it should be mentioned that the territory defending males developed a particular colouration, in which the flanks and back became brownish or dark grey, while the tip of the nose was in many specimens almost white. The females had silvery flanks, and the dark colour of their back was much lighter that that of the males. These colour differences can be seen in the figures 1, 6, and 7. Those males that had no territories were much paler than the territory guarding males.

5. Courting and Spawning

As mentioned, no spawning took place in the Hölle tank, nor did the grayling spawn in the Hegledbäcken tank as long as the bottom material

was arranged in such a way that it formed an even surface, though several spawning acts were seen in the brooks during the same period. The territory defending males in the tanks attacked the females and did not tolerate them in their territories.

Close field observations at the Svartbäcken and the Hegledbäcken revealed that the females were tolerated in the male territories only at the moment of the actual spawning, that between the spawning acts the females hid under overhanging banks at the edges of the stream or behind stones and other screening objects where they often formed small groups or schools, and that almost all spawning acts took place on the top of gravel banks, in swift current and in water so shallow that the backs of the spawning fish were often visible over the water surrace. Over the top of a bank where several spawning acts were observed in the Svartbäcken, the velocity of the stream was about 0,75 meters per second.

After these observations had been made, the bottom in the Hegledbäcken tank was rearranged on May 30th, as mentioned in the previous chapter. A gravel bank was built in the middle of the tank, dividing it into an upstream and an downstream pool. The velocity of the water streaming over the top of the bank was about 0.5 m/sec., and the depth at the apex of the gravel mound was about 5 cm. In the bottom of the downstream pool, close to the outlet of the tank, we dug a rectangular pit, about 15 cm deep and 35 cm wide.

It was thought that the females would dwell in this pit until they were ready to spawn. This arrangement did not work well, however. As mentioned, two males began defending territories in the tank. One of them had its territory in the downstream pool, and this male took its »station» at the edge of the pit. From this position it watched the females, and attacked them as soon as they moved. As a result of these attacks, the females soon became totally apathetic, and no spawning took place.

On June 1st, the pit was filled in with gravel, and a gallery of caves was built along the whole rear wall of the tank, using slatestones from the brook (Fig. 1). This arrangement turned out to be successful. The females moved into the caves, where they were not attacked, because they were not visible to the males, and they did not leave their shelter until they were quite ready to spawn, which they showed by a special signal posture.

The first spawning act was seen 6 hours after the caves had been made, and during the following days a great number of spawning acts were watched. This made it possible to make very close observations on the spawning in the Hegledbäcken tank.

Females that were almost ready to spawn often showed a very aggressive behaviour. They attacked other fish, males as well as females, and they repeatedly moved up on the top of the gravel bank, approaching the resident male. As he aproached them, they responded by erecting their dorsal and

pelvic fins, and an act of mutual lateral display followed, usually ending in a fight in which the female was driven away and disappeared into the caves.

Sooner or later, the ripe females became less aggressive, and while approaching the males, they showed a peculiar posture, in which the back was arched and the dorsal fin was pressed down (fig. 6.). This posture is very similar to the posture which the female char adopts when searching for a nest site, but unlike the char, the female grayling does not swim about at the bottom in a searching manner, but she approaches the male. Her posture of readiness apparently suppresses the aggressiveness of the male. He approaches her, presses his flank against her and trembles, as in the aggressive lateral display, but he does not erect his dorsal and pelvic fins, nor does he bite her. This apparently is the courting act of the male. On the first occasions this happens, the female usually glides away and flees, but sooner or later she remains on the bank, and a mating act follows.

The intensity of the trembling in the male increases to a very swift vibration, while he gradually erects his dorsal and pelvic fins to their fullest extent and tilts over on his side, covering the female's back with his big dorsal fin and part of his back. He also bends the caudal part of his body laterally in such a manner that it crosses over the tail of the female, pressing it down against the bottom. In this posture, the bodies of the two fish form an »X», and the body of the male is laterally bent in an S-shape, in a manner resembling the posture of a nest-digging female trout, salmon or char. The trembling of the male is accompanied by vigorous flapping movements of his tail fin, which is kept in a more or less horizontal position, close to the ground. The anterior part of the male's dorsal fin is firmly pressed against the back of the female in front of her dorsal fin, in a »clasping» way, while the posterior part of it covers the anterior part of the female's dorsal fin. It thus seems as if the big dorsal fin of the male grayling would have the double function of a signal, shown in the lateral display, and a clasping organ, used in the mating act.

While the male performs these activities, the female starts trembling too, erects her dorsal and pelvic fins, and adopts a peculiar posture. Supporting herself on her pelvic fins, she bends the caudal part of her body very sharply dorsoventrally in such a manner that her anal fin is pressed down against the ground, while her tail and the fore part of her body are lifted. As can be seen in fig. 7, this posture has great similarities to the posture that female char and brown trout adopt in »anchoring» and spawning (cf FABRICIUS and GUSTAFSON 1954, fig. 10 and 11 and JONES and BALL 1955, plate I, fig. 5), though the bending of the caudal peduncle is much more pronounced in the grayling. The clasping action of the male is much facilitated by the maximal erection of the female's dorsal fin.

In this posture the female performs very intense vibrating movements, as a result of which the caudal part of her body, working like a boring machine,
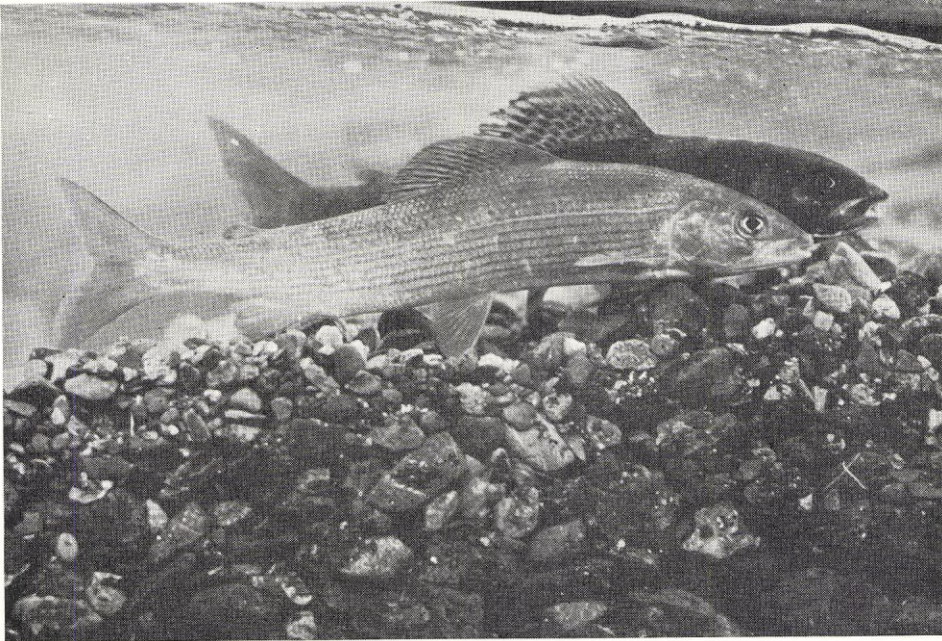
Fig. 6. A female showing the posture of readiness. The back is arched and the dorsal fin is pressed down. The dark fish behind the female is a courting male. He is still slightly aggressive, which is shown by the partial erection of the dorsal fin and the display of the black patch on the throat. Photo: K.-J. GUSTAFSON.

sinks down into the bottom material, often so deeply, that the adipose fin disappears under the gravel. She bends her caudal peduncle more and more, so that her tail finally points straight upward, and her movements are so powerful that stones are flung up, and in shallow water one can see a fountain of water over the spawning couple. In making the film, this caused us a lot of trouble, because the bulbs over the tank burst when hit by the water jet produced by the spawning grayling.

One gets the impression that the vibration of the female and the tail flapping of the male loosen the bottom material and make it possible for the caudal part of the female's body to penetrate deeply into it, while the loosened material is flung up by the upwards directed water jet produced by the tail fin of the female.

When the vibrating movements and the bending of the caudal peduncle reach their maximum, the female opens her mouth wide, and keeps it open for several seconds. This, apparently, is a signal which provides one of the stimuli which release the orgasm in the male. Some seconds after the female has begun her gaping, the male suddenly opens his mouth too, and a simultaneous orgasm follows in the two fish. By a sudden flick, in which also

the male sharply bends his caudal peduncle dorso-ventrally and lifts his tail fin, the two partners, standing side by side and often mowing slightly backwards, push their genital openings deep down, releasing a portion of their sexual products. The milt could sometimes be distinctly seen, but the eggs were usually invisible, because the anal part of the females body was hidden in the gravel. As mentioned, both sexes gape during the orgasm, quite like salmon, trout and char, but the gaping of the female grayling lasts several seconds, while the male opens his mouth for only a fraction of a second, just at the moment of the actual orgasm. We do not know whether the female grayling, perhaps, starts to shed her eggs as soon as she opens her mouth, before the male has ejected his milt. Before and after a spawning act, one can often see several incomplete acts.

The average length of 20 timed spawning acts was 14 seconds (6 to 23 sec.). During the comparatively long spawning act, the grayling are unable to observe an enemy, and it is easy for a man to approach them very closely, and to catch them by throwing a net over them. Immediately after the orgasm, the fish straighten their bodies, losing their contact with the bottom, as well as with each other. After this, the male usually attacks the female. On this attack, she often flees into some cover, leaving the male alone in his territory. Sometimes, however, she remains on the gravel, withstanding the attacks of the male, and a series of fierce fights and lateral displaying follows. After some time the female again adopts her posture of readiness, arching her back and pushing her dorsal fin down, and approaches either the same male, or some other male, for a new mating act. Very ripe females maintain their posture of readiness even when attacked by other females. When timing a series of 72 spawning acts in the Hegledbäcken tank on June 2nd, we found that the intervals between subsequent acts had an average length of 13.5 min. (1 to 74) in males, and 16.3 min. (2 to 56) in females.

The sequence of actions described above was seen in most of the spawning acts we observed in the brooks, as well as in the Hegledbäcken tank. There were some exceptions, however. In some few cases we observed that a female, like a female char or trout, started trembling and adopted the crouching posture in front of a male before he had approached her, and the male then darted to her side, whereupon a spawning act followed. Probably the mating drive had reached a very high degree of intensity in these females, and at least in some of these cases the male did not approach them immediately because he was occupied by fighting a rival, or by courting another female.

In the Hegledbäcken tank, the territories of both the spawning males were situated on a gravel bank, and thus the male and the female were already on an optimal spawning bottom when they approached each other. In the natural spawning streams, and particularly in the Hegledbäcken, the stations of the territory quarding males were in many cases not at places with a gravel bottom. When a ripe female, showing her posture of readiness,

Fig. 7. A spawning act. The light fish nearest the front pane is the female. The male, who is partly visible behind the female, is clasping her by his dorsal fin. The female is gaping. The caudal part of her body is bent, and by a vibrating movement it is being worked down into the gravel. Note the stones that are flung up. Photo: K.-J. GUSTAFSON.

appeared into the territory of such a male, he left his station, approached her, and then the two fish, side by side, trembling against each others flanks, swam to a gravel bank, where the spawning took place. To reach the bank, they sometimes had to travel a distance of about two metres. It was not possible to decide whether the swimming to the gravel bank was directed by the male or by the female, and the selection of the spawning bottom by grayling should be subjected to a more detailed analysis.

On examining the spot where a mating act had taken place, one could sometimes see a nest pit, about 5 cm wide and 3 cm deep, but in other cases it was not possible to discover anything else than an even surface of gravel. No eggs were visible at the surface, but if the stones and pebbles were removed, the eggs were found buried under them, to a depth of about 4 cm. Immediately after the spawning, the eggs stuck slightly to the stones, but they soon lost their adhesiveness, and many eggs were carried away by the current when the bottom material was disturbed by subsequent spawning acts. Most of them, however, remained in the gravel, and after some days of intense spawning, the whole gravel bank in the Hegledbäcken tank was seeded with grayling eggs. This was also the case with the best spawning banks in the streams. In the Svartbäcken we could collect large numbers of eggs at a bank where many spawning acts had been observed. When we

stirred the gravel on the bank, keeping a fine net downstream of it, the eggs emerged and were carried into the net.

In the females, the whole length of the period during which spawning acts occurred varied from about 10 hours to about 3 days. The two males in the Hegledbäcken tank spawned for 4 days, but in the streams some males were seen spawning every day for about one week. The total number of spawning acts performed by a fish varied between 18 and 34 in the females. Of the two males studied in the Hegledbäcken tank, male »A» performed 78 spawning acts, of which 60 were seen during one day, on June 2nd, whereas male »B» performed 23 spawning acts, 20 of which occurred on the intense spawning day of June 2nd.

Some homosexual spawning acts were seen, between males as well as between females. In the acts between females, one female tilted on her side over another female, performing the normal male spawning movements, while her partner performed the female spawning movements. In the acts between males, one of them tilted over on his side, trembling against the flank of his partner, who responded by an intense trembling, but he did not push the anal part of his body down into the gravel like a female. We do not know if the homosexual acts were complete, for no sex products could be seen. The movements of the fish were so powerful, however, that stones were flung up, as in normal spawning acts. In the acts between males, the flinging up of the stones must have been the result of the activity of the active partner, performing the normal male spawning movements, which thus are shown to contribute towards the »digging» of the nest.

In most cases the homosexual spawning acts occurred on occasions when a fish, resting on the bottom did not respond by moving away when another grayling approached it and trembled against its side in an act of lateral display. The intensity of the trembling then increased, and the behaviour of the active fish turned into courting and mating. This indicates that in grayling, as we have found in char (FABRICIUS 1953), brown trout, atlantic salmon and brook trout (FABRICIUS, unpubl.), the situation with a fish resting on the bottom provides some of the sign stimuli to which the releasing mechanism of the courting responds.

As to this mechanism, the females also seem to be stimulated by the sight of the erected fins, demonstrated in the lateral display of the males, for they repeatedly approached the males, though they were attacked and threatened by them, and it was observed that females were attracted by intense fights and mutual displaying between males.

The burying of the eggs into the gravel banks in the spawning act throws some light upon the function of the territorial behaviour in the males. Apparently the defence of territories has the function of spreading the spawning over as many banks as possible. Eggs which are carried away by the current are eaten by the grayling, and certainly also by other predators. If too many

Fig. 8. A grayling nest. The surface layer of stones has been removed to show the eggs. Photo: K.-J. GUSTAFSON.

grayling deposited their eggs in one bank, old nests would frequently be disturbed in the spawning acts, and this would mean a waste of eggs.

6. Promisquous Mating

While salmon, trout and char form pairs which, if undisturbed, keep together at least until the female is spent, and the polygamy occasionally shown by them is of a successive type (FABRICIUS and GUSTAFSON 1954), spawning grayling show an almost complete promiscuity, like whitefish (FABRICIUS and Lindroth 1954).

In the Svartbäcken it was observed that territory guarding males could spawn now with one and now with another female, and in the Hegledbäcken we observed that the females were also polygamous. On June 3rd we watched two male territories in the Hegledbäcken. The territories were situated just below a water fall, the Kvarnfallet, which formed their upstream border. They were separated from each other by a gravel bank, running in the middle of the stream bed, in the direction of the current. The bank, which reached

the water surface, was interrupted at its upstream end by an opening, which was partly covered by a dead tree branch. Through this opening the males sometimes passed into each others territories, fighting violent battles. We called the male of the left territory »A», and that of the right territory »B». At 2.30 p.m. a female came into the A territory from the downstream end, and a spawning act follwed on a small mound of gravel in the centre of the territory. After the mating act, she was attacked by male »A» and chased to the opening in the big gravel bank. She remained there for several minutes, resting under the overhanging tree branch. At 2.36 p.m. she moved into the B territory and spawned with the B male, whereupon he attacked her and chased her downstream, out of the territory. She rested behind some stones until 3.03 p.m., when she again swam up to the A male and spawned with him in his territory. She was then chased by him through the opening in the bank, into the B territory, where she was attacked by its resident male. When chasing the female, the B male moved into the A territory, and a fierce fight between the two males followed. Male »B» soon returned to his territory. The female approached the A male, but a second female came into the territory, behind the couple. She was attacked by the first female, but male »A» then attacked the two fighting females and chased them out of his territory. They moved downstream, but at 3.13 p.m. the first female again returned, this time to the B male, and spawned with him. After his spawning act a third male intruded into the B territory and was attacked by the B male, and the female was frightened away during the violent fight between the two males. During about 45 minutes of observation, she had spawned twice with one and twice with the other of two males, which defended neighbouring territories.

Similar observations were made in the Hegledbäcken tank. On June 2nd, when the spawning was most intense, there were two territory guarding males, »A» and »B», and three ripe females, »a», »b» and »c», in the tank, and in addition to these, there were three other females which now and then approached the males, but which did not spawn until the next day. The A male defended a territory upstream of a gravel bank, while the territory of the slightly smaller B male was situated downstream of the bank. On June 2nd, female »a» spawned 17 times with the A male and twice with the B male, while female »b» spawned 9 times with male »A» and 18 times with male »B». Female »c», spawned 34 times, and only with the A male. The most poloygamous female, »b», spawned alternately with the two males. The female »c», which spawned with only one male, was a remarkable exception. She was one of those females that did not flee when the male attacked her between the mating acts, but remained in his territory. There was a slight tendency towards a true pair formation, for when female »c» and male »A» were together on the gravel bank, he attacked strange females more

vigorously than her, though he also occasionally mated with some of these other females.

Between June 1st and June 3rd, male »A» was seen spawning with 6 and the male »B» with 3 females. All three of the females that spawned with male »B», however, spawned with the A male as well. It was often seen that a queue of ripe females was formed behind male »A», trying to approach him, and he spawned now with one and now with another of them. Sometimes two females simultaneously pushed themselves against him, one on each of his flanks.

The spawning of grayling has some similarities to the activities on the »leks» of the black cock, the ruff and some other polygamous species of birds, in which the males defend small territories which the females visit only for performing the mating act (SELOUS 1906, 1907, 1909, 1910, LACK 1939, 1946, HÔHN 1953, and others). As already mentioned, the vibrating display of the male grayling could be compared with the display postures shown by the males of these birds.

7. Some Observations on the Daily Rhythm of Activity in the Spawning Grayling

From May 28th to June 3rd, 1955, we watched the behaviour of 9 males which defended their territories in the Hegledbäcken, in a section which had a length of about 23 meters. It was observed that all these males abandoned their territories at about midnight, but re-occupied them every day, usually in the afternoon. At 8 a.m. no fish were ever observed fish in the territories, but some of the males could be found resting at a place where a number of dead trees lay across the stream, and the current was comparatively slow. The first males usually appeared in their territories between 9 and 11 a.m. Most of the territories were re-occupied between noon and 1 p.m., but sometimes it was not until about 4 p.m. until all the males were in their territories. Also in the tanks, the fish were comparatively inactive during the morning hours, and the most intense defending of territories was seen in the afternoon.

All spawning acts we observed, in the streams as well as in the Hegledbäcken tank, occurred in the afternoon or in the evning. The earliest spawning acts we saw took place at 12.35 p.m., in the Hegledbäcken tank on June 2nd, and at 1.15 p.m., in the Svartbäcken on June 3rd.

The table on p. 94 shows that after noon the intensity of the spawning rapidly rises to a maximum, which is reached at the time the water is warmest, and then it gradually decreases in the evening. As the spawning, as well as the defence of territories, apparently showed about the same daily rhythm in the natural streams, where the fish were subjected to daylight, and in the Hegled-

Tab. 1. Number of spawning acts observed in the Hegledbäcken tank on June 2nd, 1955. The water temperature was recorded at the middle of each two hour period.

Time	Temp. degrees C.	Spawning acts	Defence of territories
6— 8 a. m.	+ 4.0	—	Not yet shown
8—10 »	+ 5.8	—	Weak tendencies
10—12 »	+ 9,1	—	Intense
12-- 2 p. m	+10.5	11	»
2— 4 »	+11.6	16	»
4— 6 »	+10.5	27	»
6— 8 »	+ 9.1	17	»
8—10 »	+ 7.5	7	»
10—12 »	+ 6.0	2	»

bäcken tank, where from about 7 a.m. to about midnight they were subjected to an almost constant artificial light, we suppose that the daily rhythm of water temperature, which is very marked in the shallow brooks, is the most important of the stimuli affecting the timing of the rhythm of spawning and defence of territories in the grayling. The rising temperature during the day seems to stimulate these activities.

As shown by GUSTAFSON (op.cit.), the migratory behaviour in the grayling also seems to be stimulated by a warming up of the water, for the migration into the Svartbäcken was more intense in warm weather than in cold. Probably the light is also of importance for the migration, for GUSTAFSON found that the most intense migration took place between 4 p.m. and midnight, that is at a time when the water temperature was falling.

Some interesting observations on the importance of light were made in the Hölle tank, where the fish were subjected to daylight and no artificial light was used, and there were no marked daily changes in the water temperature, becuse the water was taken from the deep reservoir of a hydroelectric power station in the great river Indalsälven.

Every evening, at about sunset, it was observed that the current began carrying the territory guarding grayling in the Hölle tank backwards, tail first. This happened though the water temperature and velocity of the current were constant. The fish at first corrected this drift by swimming upstream, returning to their territories, but they were carried backwards again and again, and for longer and longer distances. Sooner or later they were carried to the downstream end of the tank, and on their way, some of them turned round and actively swam downstream. At the downstream grating they formed a school, and, keeping well together, this school then swam for some minutes to and fro through the whole length of the tank, whereupon the fish sank to the bottom, taking up resting positions there for the night.

Most probably a rising water temperature stimulates all the reproductive behaviour patterns of grayling, including the spawning migration as well as

the territorial behaviour and the actual spawning, whereas intense light stimulates the defence of territories and the spawning, but temporarily inhibits the migration. On the other hand, the light probably also stimulates the migratory behaviour in an indirect way, by affecting the production of some hormones.

8. Some Environmental Factors of Importance for the Spawning of Grayling

The spawning territories of grayling were usually situated in shallow pools where the velocity of the current was moderate, and stones as well as gravel banks occurred. No territories were found in steep rapids, nor in deep pools with mud bottom and a very slow current.

The average size of the 9 territories we studied in the Hegledbäcken was 2.6 m² (0.8 to 5.0 m²). It was observed that the boundaries of the territories were always formed by distinct objects, such as rows of stones, gravel banks, logs, or dead windfallen trees, which screened them off from the neighbouring territories. As the stream was not broader than one to two meters, most of the territories extended across the stream bed, from bank to bank.

The territories were much smaller at places were there was an effective screening off by obstacles than at localities where there was an even and open bottom surface. Two of the smallest territories, measuring 0.8 and 1.5 m², were found below the small water fall Kvarnfallet, described at p. 91, and this was the only place where two territories were situated side by side. In this case the screening off was very complete. The two territories had an almost rectangular shape. Their upstream ends were formed by the foot of the water fall, and in each of them one side was formed by a bank of the stream. The other side was formed by a long gravel bank, separating the two territories from each other and situated in the middle of the stream bed, whereas a log, lying across the stream, formed their downstream ends. Each of these two territories thus formed a more or less closed basin. Some other very small territories were screened off from each other by windfallen trees, lying across the stream. The largest territory we observed, measuring about 16 m², was situated in the Svartbäcken, in a shallow pool with an even gravel bottom.

It thus seems obvious that, as shown also in the aquarium experiments (p. 83), the amount of visual isolation from the neighbours is of great importance in determining the size of the territories. As has been pointed out by FABRICIUS (1951), a considerably larger number of territories may exist within an area which can be divided by ground obstacles into a number of fields, visually isolated from each other, than in an area that is more open.

As already mentioned, all spawning acts observed in the streams took
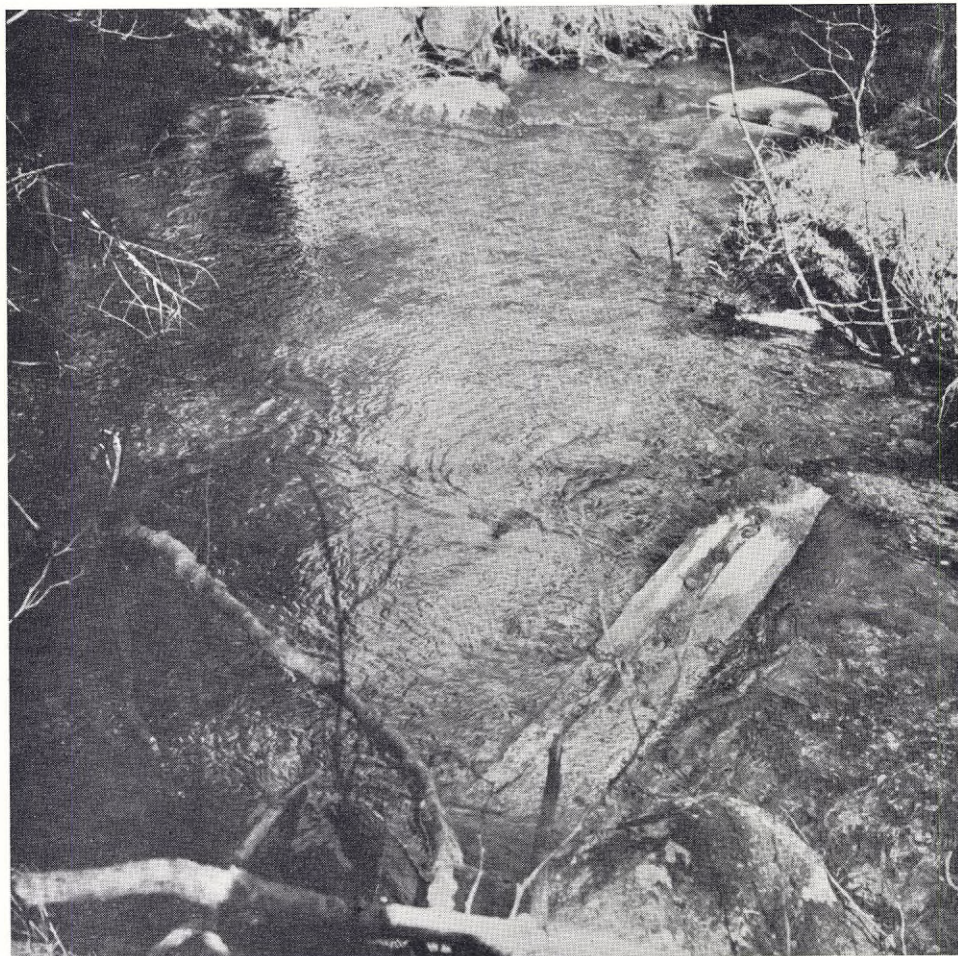
Fig. 9. A typical grayling territory in the Hegledbäcken creek, seen from the upstream end. The log in the foreground and the row of stones in the background formed the boundaries of this territory. The spawning bank was situated to the left, between the overhanging tree branch and the stone. Photo: K.-J. GUSTAFSON.

place on gravel banks. There was a gravel bank in every grayling territory we studied, and this spawning bank was always visible from the station of the male. In most cases the bank was situated upstream of the station, but sometimes it was at one side of it. Some of these banks on which the grayling spawned were quite small — only about 0.3 m². These banks consisted of comparatively fine gravel, in which most of the pebbles had a diametre of about one centimeter, and very few were larger than about three centimetres in diameter. One could call it »gravel of pea-size». The gravel bank in the Hegledbäcken tank, on which the grayling spawned, was made of gravel from

Fig. 10. A part of the same territory as shown in fig. 9., seen from the downstream end. A male grayling is courting a female on the top of the spawning bank, which is visible to the right. Photo: K.-J. GUSTAFSON.

a natural spawning bank in the Hegledbäcken. It should be mentioned that most of the spawning grayling we observed had a body length of 20 to 30 cm.

Of the 20 spawning acts we observed in the natural streams, 17 took place on the top of gravel banks, in water so shallow that the backs of the fish were visible above the water surface, whereas only 3 spawning acts were seen in somewhat deeper water, at a depth of 20 to 25 cm. In a series of 26 spawning acts in the Hegledbäcken tank, 11 occurred on the top of the bank, at a depth of about 5 cm, whereas 9 took place in the upstream and 6 in the downstream pool, but none of them at a greater depth than about 15 cm. It thus seems obvious that the spawning grayling prefer shallow places where there is a swift current of water over the top of a bank of fine gravel.

Several field observators have pointed out that salmon and trout usually chose the sites for their redds towards the downstream end of a pool (HOBBS 1937, STUART 1953 a, b and others), and in the case of the brown trout, this has been proved experimentally by STUART (1954). The grayling, however, seems to differ from these species in its selection of nest sites, for 16 of the

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20 spawning acts we observed in the streams took place at the upstream end of a pool, just where the water passed over the top of a bank and the bottom began sloping gently down towards the centre of the pool. The reason for this apparently is that the grayling in the initial phase of each spawning act move side by side, heading against the current, and this movement takes them to the upstream end of the pool, where they stop in the shallow water on the bank separating it from the next pool above it.

Our observations also showed the important ròle of overhanging banks, dead trees and other objects as shelters where the females could hide until they were ripe enogh to suppress the aggressiveness of the males by showing their posture of readiness. If there were no such shelters in a brook where the male territories border on each other, the females would certainly be driven out of the brook by the fierce attacks of the males.

It has been shown by MÜLLER (1954) that the grayling is able to use the changed bottom fauna in streams that have been cleaned out for timber floating. The food supply is, however, not the only factor necessary for maintaining a stock of fish in a stream. The observations in the brooks at Lake Storsjön indicate that a good grayling stream should contain screening obstacles that make it possible for a maximal number of males to defend territories there, gravel banks almost reaching the water surface, for the spawning, and shelters for the females, and such objects, i.e. rows of big stones, windfallen trees, and gravel banks that form ridges between pools, are usually removed when a stream is cleaned out for facilitating the timber floating.

9. A Hypothesis on the Origin of the Courting Tremble and the Nest-Digging Movements in Salmonid Fish

It is a well known fact that salmon and trout surmount water falls by jumping. Whitefish, grayling and char, which do not jump, show another type of behaviour when passing over obstacles in streams. If migrating fish of these species are caught in a weir at the mouth of a stream into which they have just entered, some specimens continue to show migratory behaviour, at least for some days, when introduced into an aquarium tank. Particularly at sunset, they swim restlessly to and fro in the tank. If they meet an opaque wall, reaching the water surface, they, often without touching the wall, stop at it and adopt a vertical posture, with head up and tail down. In this position, they perform vigorous swimming movements, in which the body makes very rapid lateral undulations. These movements are so powerful that the fish is pushed up over the water surface, often so high that only the part behind the anal fin remains under the water. After a burst of these movements, the fish sinks back into the water, but the performance is

repeated again and again. In a natural stream, this behaviour would take the fish over stone barriers and riffles in rapids and small water falls. In tanks with streaming water, this behaviour is particularly shown at the upstream grating, and especially if there is a flow of water over the top of the grating. We have also seen it in a stream, in grayling that had moved against the wire netting of a trap which had been obstructed by silt and debris so that there was a flow of water over the top of it.

Slow motion films and close aquarium observations have shown that the trembling in the courting of salmonid fish is actually a lateral undulating movement. At least, this is the case in char (FABRICIUS and GUSTAFSON 1954) and in whitefish (FABRICIUS and LINDROTH 1954), and slow motion films clearly showed that it holds true also for grayling. The movements of whitefish, grayling and char in front of an obstacle in a stream have very great similarities to the courting tremble, and in whitefish it is hardly possible to distinguish between these two types of movements. Moreover, there seems to be some connection between these two behaviour patterns in the grayling. This was shown by an experiment which was repeated several times, and always gave the same result. In a shallow tank where the velocity of the water was about 0.2 m./sec. and the grayling were comparatively inactive, the sluices were regulated so that the velocity of the current suddenly increased to about 0.7 m./sec. The fish immediately responded by the rapid undulating swimming movements described above, and these movements gradually turned into the trembling characteristic of the courting and the lateral display, while the fish approached each other and erected their dorsal and pelvic fins. This was followed by outbursts of courting, threatening and fighting and in the males by a long and very intense series of the vibrating display. The vibrating display was interspaced with violent attacks on other fish, and also with attacks »on nothing», into empty space. It was thus shown that a swift current, occurring suddenly, stimulated the movements normally used for passing over obstacles in streams, and that these movements tended to turn into those reproductive motor patterns in which the fish trembles, i.e. into courting, lateral display and vibrating display.

One could, perhaps, suppose that primitive salmonids, which moved into streams for spawning, performed rapid undulating swimming movements when heading against the current, for example below a water fall, and that the trembling in courting and spawning developed from these movements, during which the males and the females often swam side by side. The withefish »still» spawn much in this manner, swimming side by side in the free water, with undulating body movements (FABRICIUS and LINDROTH, op.cit.).

In most salmonids the trembling belongs to courting and mating, but in the grayling it is normally performed in the aggressive behaviour as well, and the courting tremble differs from the aggressive tremble mainly by its greater intensity. Cases in which some motor patterns are shown in hostile

situations as well as in courtship are known also in birds, where the »choking» of the herring gull is a well known example (TINBERGEN 1952, 1953). In this connection, it might be of some interest that STUART (1953) as well as JONES and BALL (1954) have observed that the brown trout sometimes shows the trembling behaviour in hostile situations, though it normally belongs to courting. We have seen this behaviour also in the brook trout, *S. fontinalis*. It occurred particularly during prolonged and very fierce fights between two neighbouring males, and it gave the impression of a displacement activity. The attacks were now and then interspaced with trembling against the flank of the enemy, and this behaviour differed from normal courting only by the very sudden approach of the trembling fish, and by the greater rapidity of the vibrating movements. As pointed out by TINBERGEN (1952), such displacement activities can easily, in the evolution of a species, develop into new display movements, belonging to the instinct during the activation of which they occur. In this way the aggressive trembling of grayling could have developed from the courtship trembling.

If a species, in which the male and the female swim side by side during spawning and tremble like the whitefish, performed this activity on the bottom instead of in the free water, some of the bottom material would be displaced, and one would get something that could be the first origin of nest-digging movements. Actually the female char occasionally shows a type of digging in which she rests on the bottom, and performs very rapid swimming movements »on the spot», causing a jet of water which sweeps loose material away (FABRICIUS and GUSTAFSON, op.cit., p. 65). By »exaggerating» the dorsoventral bending of the caudal peduncle and the pressing of the anal opening against the bottom that occurs in the spawning act of salmon, trout and char, and by increasing the intensity of the vibrating movements in the caudal part of the females body, one would get digging movements like those of the female grayling.

To the naked human eye, the movements of the spawning male grayling look like a trembling, but when seen in a slow motion film, they have striking similarities to the nest-digging movements of female salmon, trout and char. The body is laterally bent, so that its anterior part forms a shallow arch over the female, while its posterior part is sharply bent down, and the caudal fin is kept in a horizontal position, often touching the ground. Moreover, the vibrating is most intense in the caudal part of the body, and the caudal fin flaps against the gravel, but, unlike the females of the species mentioned above, the male grayling is not propelled forward. As mentioned on p. 90, these movements are sometimes performed by the female grayling as well, though they normally belong to the male behaviour pattern. By changes in the releasing mechanism, such a behaviour could develop into digging movements like those of female salmon, trout and char. In this connection, it might be of some interest that it has been observed in brown

trout (JONES and BALL, op.cit.) as well as in char (FABRICIUS and GUSTAFSON, op.cit.) that males occasionally perform the courtship tremble against a stone, or against the aquarium wall, or even mate with such dead objects.

In this way it is understandable how a number of specialized motor patterns, serving the reproduction of the species, could have developed in the salmonids from the intense swimming movements they perform when heading against swift currents. It should, however, be emphasized that this is only a tentative hypothesis that can hardly ever be proved.

10. **Summary**

The spawning of grayling from Lake Storsjön in the province of Jämtland was studied in the field as well as in aquarium tanks with flowing water.

In the spring, the sexually mature specimens migrate from the lake into the brooks, where they spawn. Each male defends a territory in the brook. The males react to any intruder into their territories, male or female, by a hostile approach, in which they erect their dorsal and pelvic fins. If the intruder flees, the male chases and bites it. Often, however, the intruder responds by erecting its dorsal and pelvic fins, and an act of mutual lateral display follows, which is extremely well developed in the grayling. Swimming side by side the two fish head against the current, pushing themselves against each others flanks, performing vigorous trembling movements, erecting their dorsal and pelvic fins to their fullest extent, and lowering the under part of the mouth, showing a black spot in a white field on each side of the throat. Each of them tries to swim past its opponent, and to turn across the current in front of its nose. If this manoeuvre is successful, the current carries the rear fish downstream, pushing its opponent away. This characteristic fighting pattern is shown also by immature young grayling, still living in schools. If the intruder withstands, the territory owner turns its head sidewards towards the enemy and bites it, and a violent fight may follow.

Now and then the territory defending males, even in the absence of other fish, perform the so called »vibrating display», in which they erect the dorsal and pelvic fins to their fullest extent, lift the tail, and perform trembling movements.

The border lines between the territories are usually formed by rows of stones, gravel riffles, windfallen trees and other objects by which the males are visually screened off from each other. The territories are considerably smaller at places where such screening objects occur than at localities where there is an open and even bottom.

The territory defending males had a much darker colouration than the females.

Unripe females responded to the approach of a male by erecting their dorsal and pelvic fins, and consequently they were driven out of the male territories. They dwelled, often in small groups, under overhanging banks, or behind stones, windfallen trees and other screening obstacles. No spawning took place in the aquarium tanks until shelters had been made for the females.

When the female is quite ripe, she approaches the male, showing a posture of readiness, in which she arches her back and presses her dorsal fin down. The male responds by tilting over on his side, covering the back of the female by his big dorsal fin, bending his tail across the tail of the female and trembling, and a mating act follows. During the spawning act, the female bends the caudal part of her body dorsoventrally in such a manner that her tail is lifted, and works her genital opening deep down into the gravel by vigorous vibrating movements. The eggs are released under the surface of the gravel. Both sexes gape in the orgasm. Thus, the courting, the nest-digging and the mating are combined in the grayling into one action, unlike salmon, trout and char, in which they are separate activities.

The eggs are buried into the gravel, to a depth of about 4 cm. Most spawning acts observed took place on the top of gravel riffles, in water so shallow that the backs of the spawning fish were visible over the water surface. The gravel on these banks consisted of pebbles of about pea-size.

Immediately after each spawning act, the male usually attacks the female and drives her away from his territory, but sooner or later she again approaches either the same male or another one for new mating acts. The males thus tolerate the females in their territories only at the moment of actual mating. Most of the males, as well as the females, were promiscuous, spawning with several partners. A queue of ripe females could often be seen behind a male, trying to approach him for mating.

There was a marked daily rhythm of activities on the spawning grounds, as well as in the observation tank. The males usually abandoned their territories at midnight and re-occupied them in the late morning hours, or after noon. No spawning was seen before noon. The intensity of the spawning reached its maximum between noon and about 7 p.m., that is at the time when the water in the shallow brooks was warmest.

It is emphasized that in an ideal grayling brook there should be stones, riffles, windfallen trees and other screening obstacles, making it possible for a maximal number of males to defend territories, and providing shelter for the females, and gravel banks where the eggs can be deposited.

A hypothesis is discussed, according to which some of the courting and nest-digging movements in salmonids would have developed from a type of swift and »vibrating» swimming movement, shown by some species of salmonids when passing over obstacles in streams.

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Distribution Territorial Behaviour and Movements of Sea Trout Fry in the River Indalsälven [1]

By Arne Lindroth

Introduction

Little is known of the dwelling places of the salmon (*Salmo salar* L.) and sea trout (*Salmo trutta* L.) parr in the large Swedish salmon rivers. The salmon conservation plans for these rivers, now made necessary by the hydro-electric schemes blocking the rivers, demand exact knowledge of their rearing capacity for these two main species of anadromous fish. Investigations undertaken to achieve this aim have revealed many interesting details in the biology of young sea trout parr (O-group or fry).

Habitat

The river Indalsälven has a catchment area of 26,700 km² and is the fifth largest Swedish river system. Mean water flow is 440 m³/s, and mean spring flood 1,600 m³/s. There is ice cover as a rule from Dec. to April. Until the year 1954 the river was accessible for anadromous fish for a distance of 80 km from its mouth. This stretch may be roughly divided into four main sections (see Map, Fig. 1).

1. From 75 km to 45 km from the mouth, mean fall 0.6 m/km, water velocity high, water level fluctuating, stream channel winding in the broad river bed between small tongues of land and islets, bottom mostly consisting of gravel and stones often forming a pavement. (See Fig. 2.)

2. From 45 km to 25 km from the mouth, mean fall 0.1 m/km water velocity considerably lower than in Section 1, no marked stream channel the water filling up the broad river valley, bottom sandy. (See Fig. 3.)

3. From 25 km to 15 km from the mouth, mean fall 0.5 m/km, general character as Section 1.

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[1] Report from Bergeforsens Hydro-Electric Company.
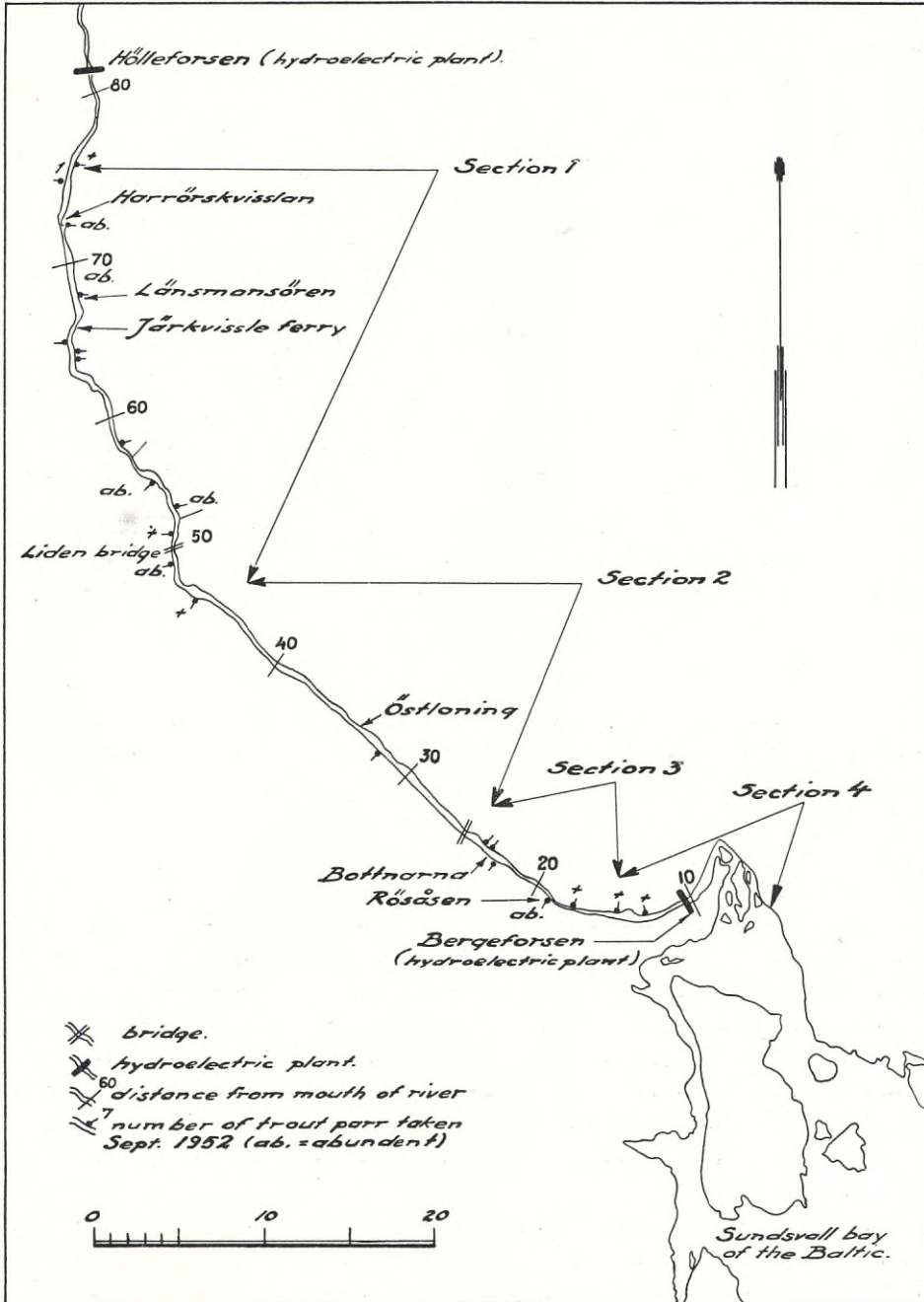
Fig. 1. Map of river Indalsälven. Distances (in km) from mouth of river and fishing results from Sept. 1952 indicated. Scale about 1 : 430,000.
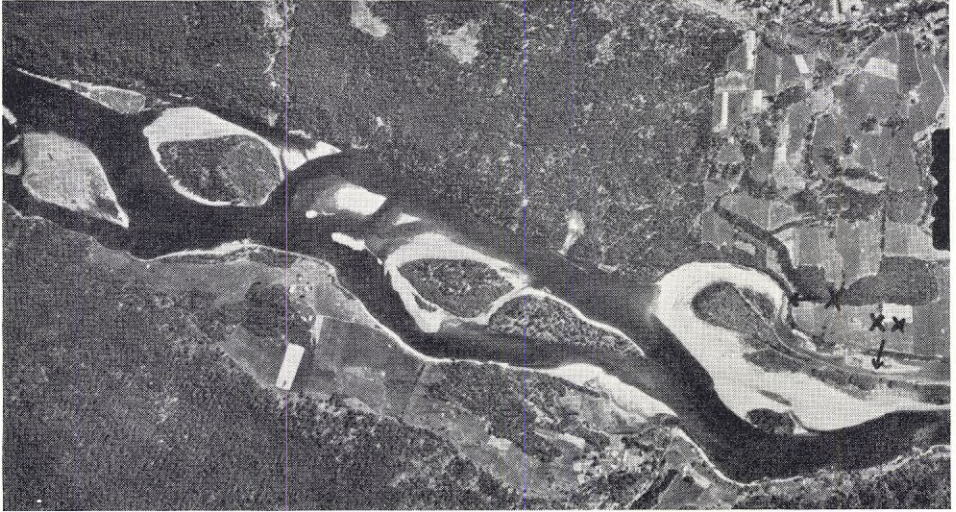
Fig. 2. View of the river from section 1. »Harrörskvisslan» is the dry branch at right where the »upper ($\times$) and lower ($\times\times$) stream» are indicated. Scale about 1 : 19,000. (Airphoto by »Rikets allmänna kartverk» 1951. Published with the sanction of »Försvarsstaben».)

4. 15 km to 0 km from the mouth, mean fall 0.1 m/km, general character as Section 2. This stretch terminates with several branches in a sandy delta.

Methods

1. Capture of sea trout parr. A very simple electric shocker was used (Fig. 5). It consisted of two 120 V dry cell batteries producing 240 V d.c. An insulated brass pipe with a switch and two brass plates about 50 cm² in area at the far end was used as an anode. The cathode was connected to a small brass wire net. During fishing the batteries were carried on the back, the cathode hung down into the water, and the anode and a dip net were held by the investigator, one in either hand. The effective catching area of this equipment in this very pure water (resistance about 25,000 Ohms/cm³ according to the season) is restricted to about 2—3 dm from the anode but it works well on hiding fish such as salmon and trout parr. The miller's-thumb (*Cottus gobio* L.), though a hiding fish as well, is not so easily caught because, on receiving a shock, it tends to spread its fins and spines and to become entangled under the covering stones. To the trained observer the hiding place of the bullhead is revealed by small clouds of mud and sand emerging from under the gravel. Fry of grayling (*Thymallus thymallus* (L.)) occasionally hide, if they do not they can only be caught after much practice. The fish on

Fig. 3. View of the river from section 2, Östloning. Scale about 1 : 19,000. (Airphoto by »Rikets allmänna kartverk» 1951. Published with the sanction of »Försvarsstaben».)

Fig. 4. Parr of salmon and sea trout, one summer old. Length 59 *viz.* 65 mm. Compare: form of head and tail; dotting of dorsal fin and white front edge of anal fin in the trout. The greater length of the pectorals in the salmon is not seen in the figure. — The figured fish have the typical appearance for the river Indalsälven. Sometimes, yet, fishes of intermediate characters may be found. (Photo: H. PETERSON.)

receiving a shock dart against the anode, if near it, becoming immobilized and swept away by the water current beyond the influence of the anode unless followed by it until netted. For this reason it is advisable to fish upstream.

Successful fishing is only possible in water from half to one meter in depth. For investigating deeper parts of the river a special method was adopted. No trout parr was ever caught in this way.

2. Marking sea trout fry. Netted fry were transferred to a small nylon netting cage until sufficient had accumulated for marking. They were first anaesthetized with ethylurethane, then measured and the adipose fin clipped. After liberation they were watched until they recovered and darted off.

3. Laboratory studies on behaviour were performed in the stream tank at the Hölle laboratory by the river Indalsäven already described (LINDROTH 1955). The dimensions of the tank are 10×1.9 m and it can be arranged so as to resemble closely a natural river in bottom and stream conditions.

General Distribution

The general distribution of trout fry along the river may best be demonstrated by the result of a three day fishing tour covering about 65 km. The localities fished and the catch are indicated on the map (Fig. 1). 65 trout parr were obtained, all but a few on river sections 1 and 3 with gravelly river bed
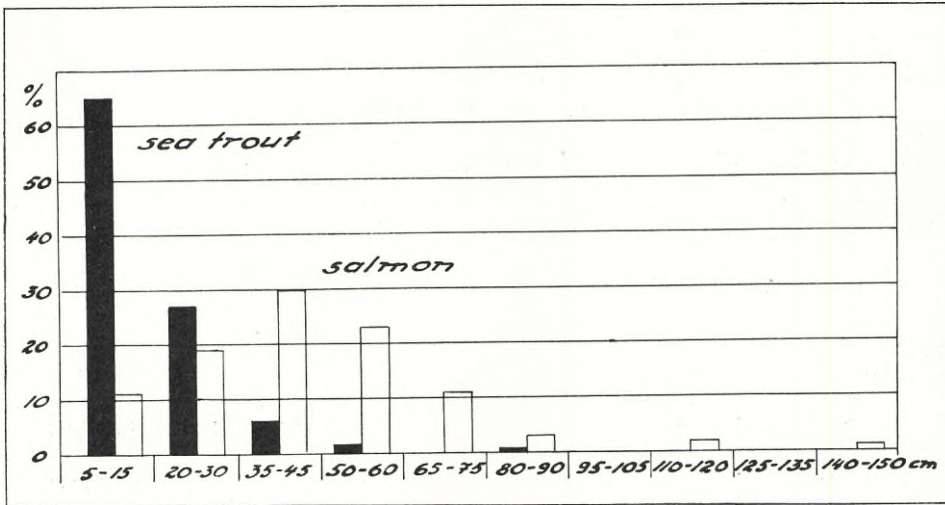
Fig. 6. Vertical distribution of young salmon and trout parr. Percentage distribution as to depth at catch in cm of 113 salmon yearlings and 195 trout yearlings made 8th March— 22th April 1953 by fishery officer N. G. STEFFNER.

and faster water current. Subsequent investigations undertaken by several investigators have confirmed the general view then obtained on the distribution of parr along the river.

On the occasion just mentioned only one salmon fry was caught. In view of the fact that the Indalsälven is a salmon river, whose trout population is of lesser importance as compared with the salmon, this may seem astonishing. The explanation for this, as suspected at the time of the investigation, is a difference in vertical distribution between the two species. The trout inhabits the narrow margin of the river down to a depth of roughly 2—3 dm, the salmon lives in somewhat deeper water. Fig. 6 illustrates this fact.

After some fishing all investigators got an eye for the trout fry localities and walking along the riverside could tell in advance where they were likely to be found. The localities consisted of stony margins or even groups of a few stones in or just under the surface of rippling water. In still water or on even, gravelly bottoms, trout parr were seldom caught. (See Fig. 7 and 8.)

The distribution relationship between trout and salmon seemed of special interest and the question naturally arose whether the two species were dependent on each other in their choice of habitat. To test this the author took advantage of an opportunity for fishing in some Norwegian salmon rivers. One of them, the river Oselva in the vicinity of Molde 170 km WSW Trondheim, was said to be almost exclusively a salmon river, poor in sea trout. During a short visit there salmon fry were caught in localities quite comparable ecologically, as far as could be judged, to those in the Indalsälven where
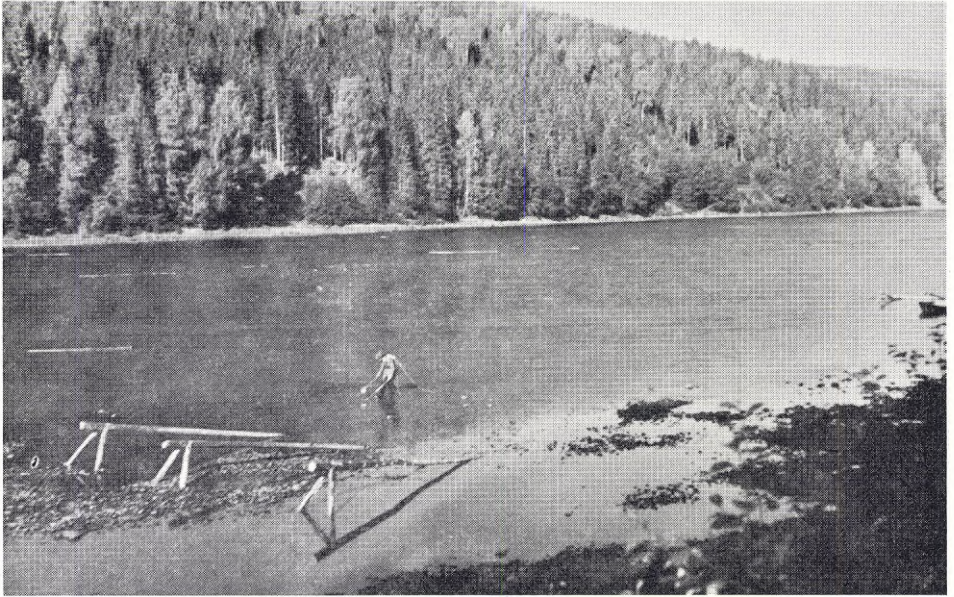
Fig. 7. Trout parr locality from the section 1 (Länsmansören). The greater stones at place of fishing about 10—15 cm. The bottom filthy of covering algae. (Note the glossy surface of some of the stones indicating that they reach above water surface.) The quiet bay in the foreground was abandonned by the trout parr but might contain some miller's thumb and minnows. (Photo: H. PETERSON Sept. 1952.)

the trout fry are found. (See Fig. 9.) Only one trout fry was caught. Repeating the fishing some days later in the Sandvikselva, a river close to Oslo with rich populations of both species, the well-known border line between the trout along the margin and salmon in the deeper water was again found with astonishing promptness. This indicates a typical case of competition possibly with a tendency to amensalism (cf. ODUM 1953), the trout occupying the most
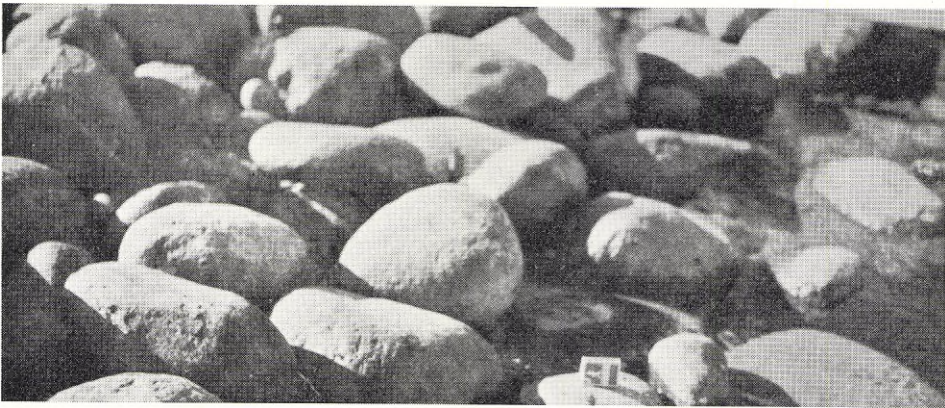
Fig. 8. Another trout parr locality, from the section 3 (Rösåsen). Only at the stony tongue parr was found. In these places also older parr are dwelling.
(Photo: H. PETERSON Sept. 1952.)

suitable localities (see further below: Territorial behaviour) leaving the remaining localities to the salmon. This theory may throw some light upon the general distribution of salmon and trout in rivers and small streams — in Northern Sweden salmon do not generally inhabit the smaller streams — and may explain why in some places a river can be a salmon *or* a trout stream — and change in this respect — but not hold good populations of both. In the larger Swedish rivers there is apparently room for them both.

Fig. 9. River Oselva in Norway. Here salmon parr resides on localities which in Indalsälven are occupied by the trout. (Photo: A. LINDROTH Aug. 1953.)

Investigators of the feeding habits of salmon and trout parr have now and then drawn attention to higher percentages of terrestrial organisms in trout as compared with salmon (ALM 1919, FROST and WENT 1940 — R. Liffey). The general impression from the Indalsälven material (not yet thoroughly worked up) corroborates this statement for this river. As pointed out by FROST and WENT, results are only valid for the particular river studied and FROST has later (1950) been unable to find differences worth noting in the food of the two fishes in the river Forss. Yet, the observed differences may be correlated not primarily with differences in food preference but with differences in habitat (cf. ALM 1919 for older parr), the trout fry living in shallower water and close to the riverside where aerial organisms may be concentrated by the wind giving the fry a better opportunity for catching this type of food. The better growth of trout parr known to salmon and trout rearers and demonstrated by several authors (ROSÉN 1918, ALM 1919 and others) may have something to do with the circumstances mentioned, to the extent innate properties or the simple fact that trout spawn and hatch earlier are not responsible.

Frequency

As the fishing did not give a 100 % yield in the areas fished, a reliable estimate of the frequency could not be obtained. A suitable place could give about five one-summer-old parr per m² as a rough figure. An overall figure for the trout stretches of the river is not easily given. Furthermore it seems to be more satisfactory to give such a figure not per m² but per m of the river bank. In good localities in the river proper, figures of about 1 one-summer-old parr per m length of bank may be found and it is probable that the mean frequency lies close to that figure for river stretches 1 and 3. In special places a greater concentration could be encountered, for example, at Harrörskvisslan with 3—4 per m of bank.

Territorial Behaviour

Our field observations have confirmed the well-known fact that trout parr are territory-holding. On one occasion, June 23rd, some trout fry were seen distributed in about one m² kept under observation. They held their positions for longer or shorter periods, always facing the stream, which occasionally at this particular place reversed direction. Chasing was observed but not always or immediately released by other fish approaching.

Further observations on the territorial behaviour of trout parr were conducted in the stream tank. The tank was furnished with a natural river bottom of gravel, stones and, in one part, sand. On July 15th 41 sea trout fry were placed in the tank together with salmon parr, grayling parr, some minnows and miller's-thumb. The sea trout were a little larger than the salmon of the same year class, as is also the rule in the river.

During the first few days there was a marked tendency for the trout fry to seek hiding places but this tendency gradually vanished, only being revived when the fish were frightened. In the river you may watch an area holding many parr for a long time without seeing a single one of them. The hiding reaction seems to be conditioned by disturbance, e.g. predators (see LINDROTH 1956).

Another general factor influencing the territorial behaviour in trout as well as in salmon parr is stream velocity. When the velocity was reduced in the stream tank from a high rate to nearly nothing the fish, at first hidden among the stones, came to the surface of the gravel, resting there in a typical manner, the lowered stream velocity causing them to leave the bottom and stay in the free water and swim in alarm to and fro in the still water.

These two facts demand caution when interpreting observations on territorial behaviour made in aquaria.

There was, however, an indisputable tendency in trout parr to hold and defend territories but it was also clear that not all parr behaved in this way

and the conditions regulating this behaviour were not studied more closely. Among the above-mentioned species in the tank the trout, or at least the bigger of them, were the most aggressive individuals. Other fish were chased and nipped. The salmon fry were regularly chased and the same was the case with the minnows. Trout have even been watched nipping a miller's-thumb and a one-year-old salmon parr but these two, or at least the first-mentioned, usually chased the trout parr for the purpose of feeding. Exact observations on the duration of a territory were not made, apparently the same fish could occupy the same place for days.[1]

The choice of holding places was very varied partly owing to the two facts just mentioned. It could be a hollow under a stone, the downward directed stream behind a piece of gravel, the water cushion in front of a large stone and so on. The general impression obtained after watching the tank frequently was that the one-year-old salmon (only a few in the tank) and the trout fry chose first while the smaller salmon fry had to take what was left. In the tank it happened to be the shallower parts, which were *not* chosen by the trout. Consequently the youngest salmon parr were common there. This behaviour, a little astonishing in view of the conditions in the river, may be explained by the bottom conditions. In the tank the shallower areas consisted of fine gravel in a thin layer on a wooden floor, the deeper parts were more varied with sand, gravel and stones. In the river, on the other hand, the stones lie near the margin and the more even gravel begins in deeper water.

The observations previously mentioned refer to the active period of daylight in summer. During the night the parr, watched in the tank, go to rest on the bottom — probably *in* the bottom as well — where they can be seen rocking motionless in the flowing water when the light is switched on. After few minutes they have resumed full activity.

Winter conditions at our latitudes mean short days, cold water and ice cover. Occasional observations in the stream tank indicate that salmonoid parr seek cover in the bottom gravel to avoid the severity of winter but on the other hand electrofishing in winter has revealed trout parr in their ordinary localities and with ample signs of feeding activities (see also MACIOLEK and NEEDHAM 1952).

Although the studies reported here have so far yielded no definite information about the significance of the different factors regulating the territorial behaviour of trout parr, they have at least demonstrated that the habit to hold

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[1] Though I can corroborate STUART's statement in his very interesting studies (1953) that trout parr tend to live less bound to the substratum than salmon, the agreement in behaviour between the two species as found in the stream tank studies seems to be extensive and I have no notation about gregarious behaviour in salmon parr except for the instances when the water flow stopped (in small rearing lakes that can be drained salmon fry are also observed shoaling). Trout parr also behaved then in the same manner. In our river we have never met with a salmon parr shoal. Territorial behaviour with nipping and dispersion appear to characterize both species as studied in our material.

territories is not a spontaneous but a reactive behaviour (cf. TINBERGEN 1951) the release of which is modified, favoured or counteracted by environmental stimuli among which stream and bottom conditions seem to be the most important.

The fact just mentioned is especially important for a fish living in shallow areas of water, whose level is rising and falling not only because of natural variations in water flow but also according to the regulation of the water for hydro-electric purposes. As a rule there is, except in summer, a daily fluctuation of the water level varying in degree according to differences in water flow, distance from the regulating hydro-electric plant and the form of the river section. The consequence is a daily horizontal displacement of the trout fry localities, which may amount to 10 m or more. These conditions would make a fixed territory-holding habit a menace to its possessor. The mechanism by which the trout fry avoid this is their reaction to the stream velocity mentioned above. With falling water level small bays are formed and enclosed. As long as water is flowing over the bottom the fry, trout as well as salmon, stay in their territories. With decreasing water velocity the »tie» between the fish and the bottom slackens and when the water is stationary, the little bay having only one connection with the river, the frightened fish rushes near the water surface in the direction of the draining water through the narrow channel into the river. This behaviour has been repeatedly studied in trout fry in the field and in salmon fry in the stream tank and explains why fry and parr of salmon and especially trout, which prefer the shallow water, are so rarely found dry on the bank or trapped in pools by falling water level. In contrast to the young of these two species, nearly all the other species in the river may be found dead, or doomed to death in the beak of a bird, on occasions like this: young of pike, perch, the two stickleback species, burbot, minnow, miller's-thumb, and young of whitefish and even of grayling.

Movements

During spawning time the river level is lower and the water area considerably smaller than when the hatched fry of salmon and trout are beginning to move.

Our first interest in the movements of the fry was connected with this chain of circumstances. Small fry were found in the beginning of June 1953 at high water, sometimes in apparently abnormal localities in the flooded vegetation, far from possible spawning places for the parents. It seemed likely that they actively sought the river margins and shallow water as fast as possible, as mentioned by SØMME (1948).

Some stream channels at Harrörskvisslan, dry except for a few pools of still water or pools fed with well water during summer and spawning time, flood

Table 1. Catch of trout parr at Harrörskvisslan.

Locality	Lower stream						Upper stream					
Yearclass	1951/52		1952/53		1953/54		1951/52		1952/53		1953/54	
Date	tot.	m	tot.	m	tot.	m	tot.	m	tot.	m	tot.	m
1953 4/3	—	—	—	—	—	—	very many	—	—	—	—	—
8/7	—	—	—	—	—	—	?	—	about 100	—	—	—
1/10	7	—	242	—	—	—	0	—	56	—	—	—
19/10	3	0	176	32	—	—	0	—	38	9	—	—
16/11	—	—	—	—	—	—	2	2[1]	57	16 + 4[1]	—	—
17/11[2]	—	—	—	—	—	—	0	—	8[2]	4[2]	—	—
1954 23/3	1	0	69	14	—	—	0	—	32	11	—	—
22/4	0	0	35	9	—	—	0	—	27	9	—	—
29/4	0	0	4	—	—	—	0	—	32	3 + 9[1]	—	—
1/6	0	0	10	3	0	—	0	—	5	1	0	—
13/7	0	0	24	4	2	—	0	—	4	0	1	—
29/10	—	—	4	1	75	—	—	—	0	0	15	1

m=marked before (marking only in 1953).

[1] Marked in the lower stream.

[2] The catch of 16/11 was kept in a tank over night and not liberated before the fishing 17/11 was completed.

regularly in early summer. (See Fig. 2.) In the still pools trout parr may occasionally be found but in the pools fed by springs trout parr are abundant. Obviously they must have got there as small fry during high water conditions.

In the year 1954 the spring spate was uncommonly small and did not as usual fill the dry river bed branch at Harrörskvisslan. Consequently only very few fry were found there in the middle of July that year in two specially studied localities, where they abounded in earlier summers and where that particular year 1-year-old parr were more numerous than the younger ones (see Table 1). As a rule the numbers of older parr elsewhere are only a small percentage of the fry. In August very heavy rains gave rise to a late spate flooding the dry river branch in question. Control fishing (Oct. 29th) resulted in good catches in both places and now the fry dominated. This example explains the role of the early high water in distributing the trout fry over their feeding areas in the river.

Small stony islands in the river sometimes give astonishingly meagre results with electro-fishing though, as far as can be judged, they are well suited to the trout parr. These islands are completely flooded in early summer, when the parr seek the river margins, and offer at that time no halting stimulus for the little fish. At the time when the islands emerge through the sinking river surface the trout parr have already settled at the river margins and the permanent islands.

Table 2. Finclipping experiments.

Date	Locality	One summer old parr				Older parr	Comments
		Total catch		Marked before	Marked now		
		nr	nr/m[1]				
1953							
Aug. 10th	Länsmansören	41			41		
Aug. 12th	Järkvissle ferry	8			8	1	
Aug. 12th	Länsmansmon	50			50		
Aug. 12th	Länsmansören	40		7	33		
Aug. 13th	below Liden	116			116	5	
Aug. 13th	above Liden	29			29		
Aug. 14th	above Liden	44			44		
Aug. 14th	below Liden	2			2		
Aug. 19th	Länsmansören	57		5	52		
Aug. 19th	Länsmansmon	43		1	42		
Aug. 21th	Bottnarna	39		1	38		
Aug. 27th	Länsmansören	36		4	32		
Aug. 28th	Länsmansören	37		13	24		
Oct. 1st	Harrörskvisslan	298	3.1		286	7	see table 1
Oct. 6th	Länsmansören	106	0.75	12	94		
Oct. 6th	Länsmansmon	26		3	23		
Oct. 6th	above »	18	0.23		18		
Oct. 6th	Länsmansören	41	0.55	20	21		3,5 hour later
Oct. 7th	Länsmansören	37	0.5	9	28		
Oct. 7th	Långjonke	22	0.22				
Oct. 7th	Vålören	15	0.15				
Oct. 7th	below Långjonke	17	1.7				
Oct. 7th	Nipören to Järkvissle ferry	47		3			
Oct. 9th	below Liden	19	0.19	2	17		
Oct. 19th	Harrörskvisslan	214	2.3	34	161	3	see table 1
Oct. 20th	below Liden	38	0.25	3	35		
Nov. 16th	Harrörskvisslan	57	3.86	20	35	2	see table 1
Nov. 17th	Harrörskvisslan	8		4	4		see table 1
1954	Harrörskvisslan						see table 1
Sum		1,505			1,233		

[1] Nr per m of river bank.

It is clear that vertical and horizontal movements towards and along the shore are made by the fry. An extensive fin-clipping scheme was carried out to investigate these movements of the fry in their first autumn. About 1,200 parr were marked from August to November 1953. The areas were also fished for control in 1954. See Table 2.

When beginning the marking experiment we thought the trout parr population was very stationary (see SØMME 1948, ALLEN 1951) and expected to recover the marked individuals on the marking localities. This only occurred to an astonishingly small extent. Our general experiences have shown that electro-fishing catches about 70—80 % of the one-summer-old parr in a sea trout population. Repeated fishing and fin-clipping in restricted areas ought, therefore, to yield after a few times marked specimens exclusively or nearly

exclusively — if the populations were stationary. This is apparently not the case. When the fishing has been repeated more than 2 days after a previous marking only about 10 % of the captured parr have been marked. When repeated within one day about 10 to 50 % were marked. These facts indicate a great instability in the populations, the fry apparently moving along the river bank.

Exceptions to the above-mentioned figures for recaptures are the two localities at Harrörskvisslan (see Table 1). These are two minute rapids fed by a well and separated from each other and from the river proper by pools of still water. They are situated in a branch of the river which is generally dry. Here the recaptures have amounted to 20—30 % after 19 and 28 days. In these well-confined localities the populations thus seem to be a little more stable. No specimen from the upper stream (marked through clipping the adipose as well as one pelvic fin) was ever recaptured in the lower stream but parr marked in the lower stream were on some occasions caught in the upper (in all 15 specimens).

Some recaptures of marked parr have been made at places where no marking had been performed. At Bottnarna, 23 km from the mouth of the river in section 3, one marked sea trout parr was caught 11 days after the first markings took place 45 km further upstream and 8 days after another marking 27 km upstream. At Järkvitsle färja three marked parr were caught close to a place where 8 parr were marked nearly two months earlier. In view of our general rate of recapture, roughly 10 %, at least some of these three fish must have been marked at greater distances.

A downstream movement of trout fry, established by other authors (NALL 1930, HUNTSMAN 1945), has been demonstrated in quite another way. A smolt trap in the mouth of the river has for three successive seasons caught some sea trout fry, though it is not well suited for the trapping of these small fish.

Thus, though territory-holding, the sea trout parr of the river Indalsälven are very mobile. Movements have taken place upstream as well as downstream. The natural assumption that their horizontal movements are performed in shallow water, their ordinary residence, is strongly supported by the above-mentioned observation that they are sparse at the small islets surrounded by deeper water.

It may finally be stressed once again that fluctuations in the water level are a daily event during most seasons in the Indalsälven owing to the power plants. The very shallow water habitat of the trout parr force them to leave their territories perpetually and establish new ones as the water margins move on the shore. This may well produce a stronger movement *along* the river banks than would have been the case under more stable conditions, where no external factor compels the parr to leave their occupied territories. The results presented here must not, therefore, be generalized.

Summary

The sea trout fry population of the river Indalsälven was studied by electro-fishing, marking experiments and stream tank observations.

The trout fry was found to occupy the shallow water (0—3 dm deep) border line of the river, where the water ripples over stones and gravel. Facts are presented indicating that the trout actively drives the salmon fry away from these chosen areas.

Observations in a stream tank have shown the territorial behaviour to be dependent on water velocity. This circumstance explains the field experience that trout fry are very rarely seen locked up in shore pools by falling water level — before being imprisoned they leave their territories.

Marking of over 1,200 fry showed the trout parr population to be unstable, undertaking extensive horizontal movements.

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Internal Tagging of Salmon Smolts II.[1] Method of Recapture. Returns 1954

By Arne Lindroth

Introduction

In a previous paper (Lindroth 1953) a technique for the internal tagging of salmon smolts was described. It was pointed out that returns could be expected only by examination of large landings of salmon caught in the sea, or in the home river if the catch there was concentrated to a few places. The intended use of X-rays or metal detectors was indicated.

The conditions for the use of internal tagging are fulfilled in the river Indalsälven, where over ³/₄ of the catch of anadromous fish from the season 1954 onwards is concentrated in the fishery of Bergeforsen's hydroelectric plant which is under construction and which blocks the river about 10 km from the mouth. The tagging plans have been drawn up with this fact in mind and the following tagging experiments have up to now been undertaken partly by the Migratory Fish Committee.

Year	Expt. No.	Tag type	Smolt from	Date and place of liberation	Dist. fr. mouth, km	No.
1952	6	A, B	troughs	Sept., coast outside river	—	1,113
	8 a	A	»	Sept., river	50	1,740
	b	A	»	Sept., river	65	1,610
	10	B	large pond	Oct., river	25	2,250
1953	1	C	troughs	May, river, var. places	—	9,526
	7	B	{troughs in w. Swed.	}Oct., river	2	1,200
	8	B	ponds	Sept., river	2	174
1954	1	A C	river	June, river	2	80
	4	C	troughs	June, river	50	759
	16	C	»	Dec., river	10	898
	18	C	»	(to be liberated spring 1955)	10	519

Tag types A and C were $12 \times 3 \times 1$ mm stainless steel, type B was $12 \times 3 \times 0.7$ mm. The thinner tags were often slightly bent during manufacture, with sharp and irregular edges.

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[1] Report from Bergeforsens Hydro-Electric Company.

In cooperation with the Migratory Fish Committee some batches have been marked with external tags as well in order to test the relative efficiency of the two types of tags (255 in expt 1952 6, 582 in expt 1953 1).

The first returns were to be expected in the summer 1954 when some of the smolts which migrated to sea in spring 1953 from the 1952 and 1953 taggings would normally be ascending their home river as grilse.

Method of Recapture

The choice between the X-ray technique and the use of metal detectors fell upon the former, mainly because of the better opportunity of localizing the tag in the fish body and the possible future use of tags with lead numerals directly visibly on the X-ray screen. The first mentioned reason for our choice proved to justify it.

The X-ray apparatus used comprises an onetank half wawe generator type FMK — 2 with control stand (manufact. GEORG SCHÖNANDER). Output 30 mA/85 kVP for radiography 3 mA/85 kVP for fluoroscopy. The apparatus was connected to a fish tank as demonstrated in Fig. 1. The fish were placed on a special carrier equipped with electrodes for electronarcotization. Much care was taken to reduce the water column through which the rays passed. Additional reduction of water can be obtained either by lowering the water level in the system down to the fish or by placing a rubber cushion with air between the fish and the roof of the tank. The carrier was moved by an electrically driven screw. The tank was attached to the concrete wall of an investigation chamber forming part of a large salmon trap connected to the power plant and the holding ponds for adult fish and intended to catch most of the ascending fish.

When examining a batch of fish an assistent takes them one by one and after weighing and measuring them puts them on the carrier which is moved into the tank. The investigator, sitting in the dark chamber, switches on the X-ray lamp and can follow the movement of the carrier and the arrival of the fish head first. When the fish has passed he can stop the carrier or reverse its direction, several times if necessary for close examination of suspected parts of the body. Finally he starts the carrier moving outwards, the fish is removed by the assistant, liberated if without a tag or killed for examination if a tag is observed. A tag is generally disclosed in the X-ray apparatus at once. Sometimes certain structures e.g. the vertical plan of the pectorals, may arouse suspicion but, as a rule, in these cases there is no tag. The situation of an observed tag is noted and after X-raying is complete the tagged fish are dissected to recover the tags and their position and number noted. Often the tag is easy to find. Should this not be the case the dead fish can be examined in the apparatus once again for better localization. Tags in the swimbladder
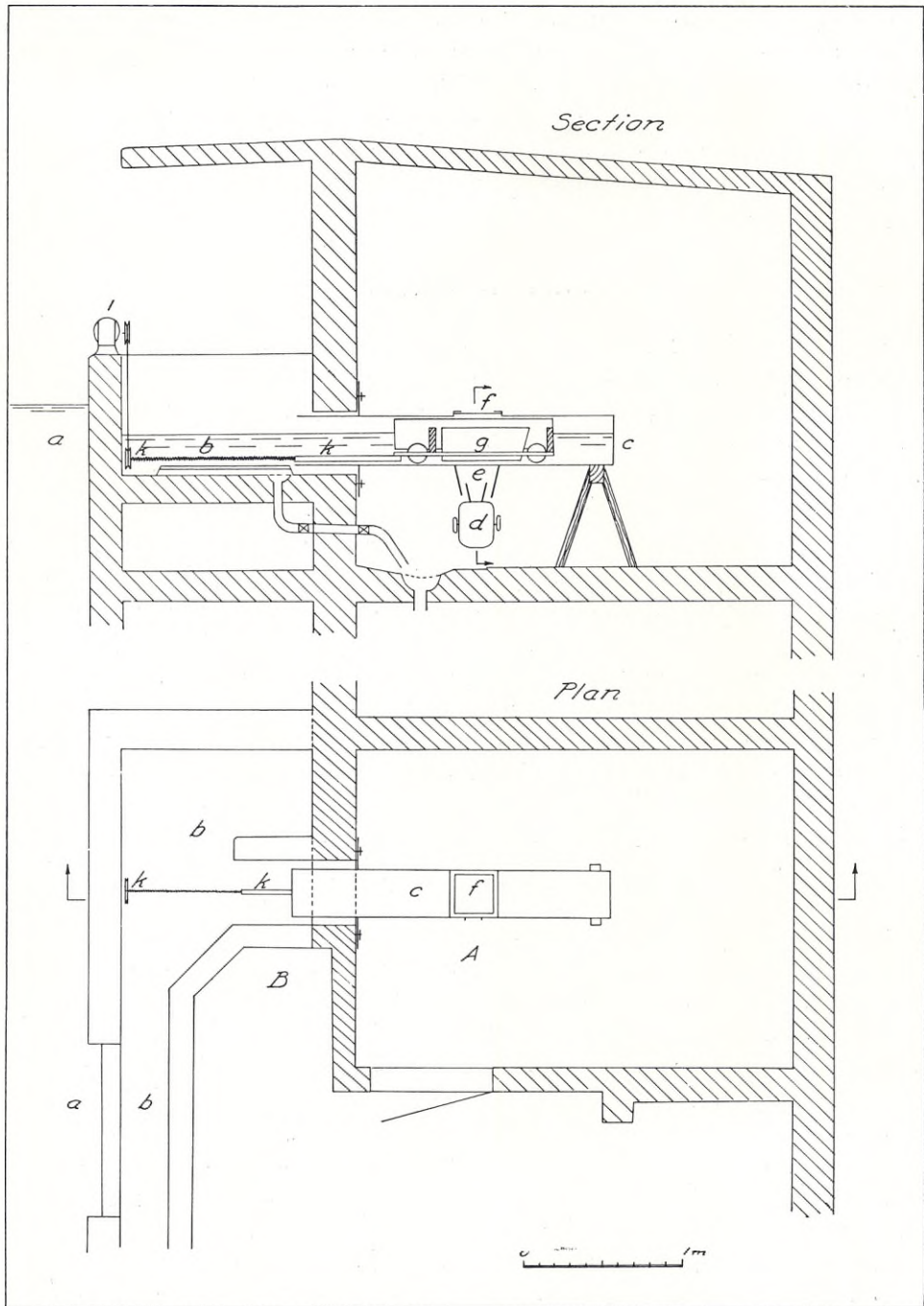
Fig. 1. Plan and section of X-ray investigation device. Scale 1:45.

A investigator, *B* assistant.

a catching basin of fish trap, *b* examination channel, *c* lead covered fish tank, *d* X-ray tank, *e* plastic plate, *f* plastic plate and X-ray screen, *g* fish carrier, *h* air, *i* fish, *k* screw and socket the latter fixed to the carrier, *l* motor.

are sometimes difficult to locate because they may alter position and in a few cases tags in the body wall could be found only after cutting the fish into pieces and X-ray examination of the small parts of flesh. On these occasions the superiority of the X-ray technique compared with the metal detector was clear.

Returns 1954

Out of 15,126 tagged parr and smolts liberated in the river some of which formed part of the 1953 smolt yearclass 89 have been recaptured as grilse out of 1,593 grilse examined in the summer and autumn of 1954.

The distribution of the returns in relation to smolts tagged and grilse caught is as follows:

Tagging year	1952				1953	Total
Tagging expt.	6	8 a	8 b	10	1	
Tagged fish	1,113	1,740	1,610	2,250	9,526	15,126
Recovered as grilse	0	10	12	20	47	89
Recovered %	0	0.57	0.75	0.89	0.49	0.59

Fishing period	July	August		September		Oct. Nov.	Total
	15—31	1—15	16—31	1—15	16—30	1—15	
Caught grilse.........	29	287	565	447	188	77	1,593
Tagged grilse.........	—	31	29	17	11	1	89
%	—	10.8	5.1	3.8	5.8	1.3	5.6

Discussion

A definite evaluation of the *method of recapture* is not practicable yet. Next years investigations will show whether it is more difficult to handle the large fish.

The *method of tagging* cannot be fully judged either. There is some indication of better returns for internal than for external tags but some external tagging experiments have yielded extraordinary good and even better returns than those in which internal tags were used.

The returns of the coming years must be awaited and more experiments performed, before we can decide if the advantages of the internal tagging are great enough to counterbalance its apparent disadvantages, namely, locally restricted possibility of returns requiring expensive and laborious work.

The position in the fish of the 89 tags recovered will be seen from the following table:

Tagging experiment	1952/8		1952/10		1953/1	
Tag type	A		B		C	
Tagger	X		X		Y	
	No	%	No	%	No	%
Tag capsuled, as a rule in the vicinity of the spleen or pyloric appendages	6	30	2	11	31	69
Tag free in body cavity	13	65	5	26	11	25
Tag in swim bladder	—		10	52	2	4
Tag in body wall embedded in muscle tissue ..	1	5	2	11	1	2
Position not noted	2	—	1	—	2	—
Total	22	100	20	100	47	100

Tag capsuled or free in body cavity must be regarded as the normal position. Tag in the swim bladder or in the body wall is not normal. It seems quite clear that whereas there is apparently no consistent difference in position in which the tag is found when tagged by different taggers, the opposite holds true in respect of type of tag. Type A and C, stamped out of 1 mm material is found capsuled or free in body cavity in more than 90 % of the cases. Tags of type B, 0.7 mm thick, often not quite regular and with sharp edges, apparently tend to move in the body often coming to rest in the swim bladder; this may be because it cannot »work» further once it reaches the gas in this organ. Though there is, remarkably enough, no indication that tags B adversely affect the fish as indicated by percentage returns of tagging experiment B (on the contrary the largest return has been obtained with this tag), it may be that the return would have been still better had tag A been used and tag type B will be avoided in the future.

Though the *biological results* of the tagging experiments will not be available for some years a few preliminary observations may be made.

All tagged salmon recaptured this year as grilse were males, though a few untagged specimens, apparently of the same age (scales not read yet) have been stripped as females.

It may be observed that there have been no returns in the river from tagging experiment 1952/6 in which the fish were liberated outside the river. There have been 4 returns reported from the Baltic, 3 through the chance discovery of the internal tags, one on account of its external tag. This result seems to possess a certain bearing upon the problem of homing instinct imprinting.

Percentage returns of parr reared and fed in troughs and of those reared in large ponds on natural food have been roughly the same. In this respect, as in the case of length at tagging, place of liberation and so on, small differences were observed which in the course of time may turn out to be significant. They are not discussed in this connection.

Finally it may be mentioned that some tags are reported from parr caught in the river before smolt migration and from grilse caught in the sea as far away as in the southernmost Baltic.
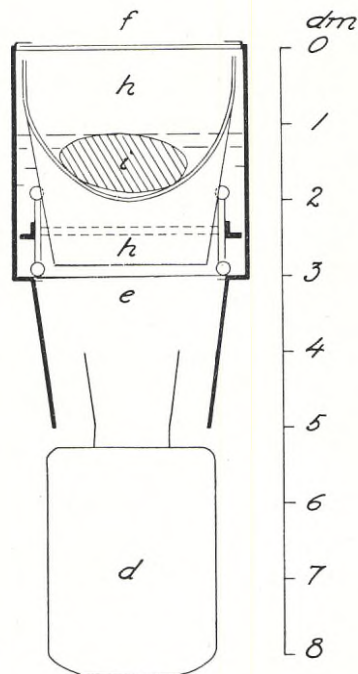
Fig. 2. Section of fish tank. Scale 1 : 10. Explanation, see fig. 1.

Summary

Salmon tagged as smolts with an internal tagging technique (LINDROTH 1953) have been recaptured with the aid of an X-ray investigation device, described in this paper. As yet only grilse have been available for recapture. In the season 1954, 89 returns were obtained out of 15,126 tagged young and of 1,593 grilse examined.

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LINDROTH, A. 1953. Internal Tagging of Salmon Smolt. *Rept. Inst. Freshwater Res. Drottningholm 34: 49—57.*

Mergansers as Salmon and Trout Predators in the River Indalsälven [1]

By Arne Lindroth

Introduction

The salmon populations of the large Swedish rivers emptying into the Bothnian bay and Bothnian Sea of the Baltic show, as demonstrated by the catch, big simultaneous fluctuations, possibly of regular periodicity of about 60 years. (See Lindroth 1950 *et. al.*) The exact cause — or causes — of this fact is obscure. There are circumstances indicating factors working in the sea where the populations from the different rivers mix in a comparatively restricted area. However, the river life may be as important a period for the action of the factors resulting in the series of bad and good year-classes.

In the salmon rivers of eastern Canada where the same *Salmo* species, *i.e. S. salar* L., occurs predatory birds have been shown to exercise a great influence upon the number of migrating smolts. A tributary to the Margaree river, N.S., increased its smolt output more than twice in response to one years control of kingfishers and mergansers (White 1939) and the Pollett river in the Petitcodiac system, N.B., yielded a 5-fold increase in smolt production from plantings after control of the same two predators (Elson 1950). Details of an economic procedure for the control of mergansers are now under development in the Miramichi river system (Elson 1952).

Of the predatory birds mentioned the mergansers are common in the Swedish rivers also and represented by the same two species, *Mergus merganser* L, and *M. serrator* L. This paper reports on an investigation made to show the role of mergansers in a Swedish salmon river.

Methods and Material

The present investigation has been carried out on the lower Indalsälven which has until recently (1954) been accessible to anadromous fish for about

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[1] Report from Bergeforsens Hydro-Electric Company.

80 km. A description of this stretch of the river is given in another paper (LINDROTH 1955) to which the reader is referred.

The field investigation was performed June 17th—July 6th 1954 by an assistant travelling down the broad river on board a rowingboat. At suitable places halts were made, frequently for several days, the birds watched and a number of them shot. Young birds and viscera of the old birds were preserved in formalin and afterwards examined in the laboratory. The contents of the ventricle were often too digested to allow the number of fish to be determined.

Results

Distribution of mergansers

The mergansers were mainly concentrated in two stretches of the river with high water velocity and a bottom of gravel with stones and coarse sand, the upper stretch about 75—45 km, the lower 25—15 km from the mouth. The fish populations in these places consisted of millers thumb (*Cottus gobio*, L.) minnow (*Phoxinus aphya* L.), salmon parr (*Salmo salar* L.), sea trout parr (*S. trutta* L.), grayling (*Thymallus thymallus* L.) and some other species, arranged in the order of their estimated frequency.

The part of the river between these stretches had a sandy bottom and a poorer fish fauna with the stream forms practically missing. The lowest part including the estuary resembled this stretch and was not included in the investigation because hardly any salmon or trout live there.

Only the larger form, *M. merganser* occurred in the upper stretch, whereas *M. serrator*, typically a coast inhabitant, was met with in the lower stretch.

Number of mergansers

A conservative estimation of the merganser population gives at least 20 breeding pairs of the larger species and considerably fewer of the smaller form. A great number which were not breeding, probably young birds, have to be added.

Feeding habits

When feeding the adult birds as well as the brood of larger young preferred not too deep water a few metres deep in the vicinity of the river banks or islands. A considerable water velocity could be tolerated. The adult bird was a very persistent fisher when undisturbed. The brood with the smaller young fed in shallow pools and bays with quiet water.

According to general knowledge and our fishery investigations miller's thumb and minnow are distributed over either types of the mergansers feed-

ing grounds whereas the stream fishes, parr of salmon and sea trout and grayling, are restricted to running water.

The result of the analysis of the content of preserved viscera is given in Table 1.

Parr of salmon and trout have been taken by the majority of the shot birds (17—19 of the 25 specimens); 7 or all adult birds (5 *M. merganser*, 2 *M. serrator*), the two big young and 8—10 of the 16 small young. Only 6 small young have with certainty not eaten salmon or trout, 3 of these belong to a brood shot in a quiet bay (Nos. 1—4) one was taken in the middle stretch of the river poor in salmonids (No. 14).

The recognizable specimens of salmon and trout have almost all been parr of one year of age or older. It is not clear if this is because the smaller fry are rapidly digested until they are unrecognizable.

One bird contained only one salmon body cavity tag, a witness of a swallowed salmon of smolt size.

Miller's thumb had been eaten by 13—16 of the 25 specimens thus a little less frequently than salmon and trout. Fry of *Leuciscus grislagine* (L.) had been taken by two young from quiet water and a lamprey by an adult bird. On one occasion an observed merganser was seen to have caught larval lampreys.

One little duckling, feeding in a shallow branch of the river was found to have eaten only larvae of crane-fly, *Tipula*.

The results show that the mergansers in Indalsälven, both the adults and the young after the first weeks, feed mainly on the type of bottom inhabited by salmon and sea trout parr and consume almost exclusively salmon and trout parr and millers thumb, principally the two first mentioned.

Discussion

The distribution of the merganser species in Indalsälven is apparently the same as in Canadian rivers, the smaller one (*M. serrator*) being concentrated in the lower parts of the river (WHITE 1939).

The food of the mergansers in the Canadian salmon rivers seems to be predominantly salmon and trout parr (WHITE 1936). Of 28 specimens examined 23 contained food including 56 yearling salmon, 9 fry of salmon, 5 yearling or older trout and 9 other fish. The salmon fry were taken by young mergansers. Other investigations have given higher figures for salmon — 91.5 % by number and a higher percentage by bulk. The predominance of older parr is in accordance with the results of the present investigation.

The Canadian investigations have lead to the conclusion that mergansers »tend to take the food most easily obtained» (TAVERNER after WHITE 1936). This statement seems to be in disagreement with the results reported above.

Table 1. Food analysis of mergansers from Indalsälven 1954.

No	Date	Place	Age	Locality	s+tr²	mth²	Lg²	Stomach, content
A. M. merganser								
1	June 20	Boda	juv.	bay			2	Small fish
2	20	»	»	bay				Empty
3	20	»	»	bay		1	1	Half digested
4	20	»	»	bay		2		Half digested
1—4¹					1?			Backbone of salmon or trout, 2 backbones of miller's thumb, caddis house, ant, insects
5	21	»	ad. ♀	flying	+	2		Vertebrae of salmon or trout, 2 miller's thumb
6	24	»	juv.	river bank	1	1		Salmon 4 cm, miller's thumb 5 cm
7	24	»	»	river bank	+	1		Miller's thumb 4 cm
8	24	»	»	river bank	2			Vertebrae of salmon or trout
6—8¹					1			Salmon ca 2.5 viz. over 5 cm, remnants of miller's thumb, insects
9	25	Järkvissle	juv.	shallow branch				Many larvae of *Tipula*
10	25	»	ad. ♀	river	2+			Vertebrae of at least 2 salmon or trout
11	28	»	»	flying	1+?	+		Tail of salmon less than 10 cm, vertebrae of more salmon or trout and of miller's thumb
12	30	Liden	»	resting	1+			One salmon or trout, vertebrae of others, one lamprey
13	July 1	Nilsböle	»	river	+			Bones and vertebrae of salmon or trout
14	2	Baggböle	juv.	river	+	1+		One miller's thumb, vertebrae of others
15	3	Arklo	»	river branch	+			Internal tag 28280
16	3	»	»	river branch	+	+		Tail and vertebrae of miller's thumb
17	3	»	»	river branch	+			Vertebrae of salmon or trout
18	3	»	»	river branch	+			Vertebrae of salmon or trout
15—18¹					6+			Remnants of at least 6 salmon or trout
19	5	Järkvissle	large juv.	resting	1+	3+		One salmon or trout, 3 miller's thumb and vertebrae of both species
20	5	»	»	resting	2+	1+		2 salmon or trout, one miller's thumb and vertebrae of the latter sp., various remnants
21	6	»	smalljuv.	river				Bones of fish, no vertebrae
22	6	»	»	river	2	1		2 salmon or trout, one miller's thumb, white larva
23	6	»	»	river	4			4 salmon or trout, insects
B. M. serrator								
1	July 3	Arklo	ad. ♂	river	1+	3		Vertebrae of one or more salmon or trout, 3 miller's thumb
2	4	Svedje	ad. ♀	river	+	4+		Vertebrae of salmon or trout and miller's thumb, 4 specimens of the latter

¹ The stomach contents were mixed before the final examination. ² s+tr salmon or trout. mth miller's thumb. Lg *Leuciscus grislagine*.

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Fishery studies extending over some years in Indalsälven have given the impression that minnows and grayling are the fish most easily seen in the river at least near its bank. Fly fishers can verify that further out from the bank grayling of smolt size is much more easily caught than salmon or trout parr. Yet none of these fish have left traces in the merganser stomachs examined in which salmon and trout parr besides millers thumb are predominant. Both the two species first mentioned are living in the free water where they are easily seen only hiding when chased. Common to the three other species is their habit of keeping out of sight close to the bottom very often under cover. Should the minnow because of its smaller size and tendency to live in shallow water be an exception to the rule at least the grayling ought to be frequently taken. This not being the case either the frequency of this fish must be overestimated or the merganser is selecting its food. WHITE (1939) reports having found mutilations of the caudal fin in parr which he supposed to be caused by mergansers attempting to pull them from beneath stones. This procedure would seem to be much more useful in the case of millers thumb — which never leaves the bottom and anchors its spines into the substratum when shocked — and the larval lamprey which is usually buried in the sand. It seems not unjustified to assume a special feeding technique for mergansers in swift running water where their manoeuvring skill may be inferior to that of the free water fishes, a technique including some kind of working the river bottom in sight of prey or at random. The assumption will if possible be tested experimentally in the stream tank of the Hölle laboratory (LINDROTH 1954).

On the basis of a consumption of 250 g of fish (salmon) per day and 7 g per salmon parr WHITE (1936) estimates the yearly loss through 100 mergansers at 0.5 million parr per year in a part of the Margaree river. Later WHITE (1939) has stated this estimate to be very conservative. He found that a nearly fullgrown merganser ate a pound (454 g) of fish each day.

A corresponding estimate for Indalsälven in the year 1954 may be based on the following assumptions.

1. 25 breeding pairs of both species with 5 young in each brood reaching adult stage and 50 not-breeding adults giving a total of 100 adults and 125 young.

2. An adult merganser needs 400 g of fish per day. The rearing of one young merganser during the summer (to Oct. 1st) requires 90 days $\times$ 200 g = 18,000 g of food.

3. Salmon and trout parr constitute 50 % of the food by weight. Mean weight of parr 10 g.

These postulates, by no means exaggerated, give for four months, June to September, $4 \times 30 \times 100 \times 400 + 125 \times 18,000 = 7,050,000$ g which is approximately 7 tons of food, 3.5 tons of parr or 350,000 parr.

In the Canadian rivers control of mergansers has yielded results promising practical and economic benefit.

In Indalsälven the mean production of smolt is estimated to be of the order of 300,000 smolts per year with considerable fluctuations around this figure. Should the maximum figures or even the mean figure correspond to the production capacity of the river without taking account of the mergansers at least the minimum figures must mean that the production capacity of the river is not utilized and the loss of parr through predators implies loss in smolt production. It may be that predation by mergansers affects the salmon and sea trout parr so seriously — as in the Canadian examples — that the production capacity is never reached and fluctuations in the merganser populations have a permanent influence — causing fluctuations in the stock of these commercially important species of fish.[1] Further investigations may throw light upon this question.[2]

In his aforementioned work (1950) the author has pointed out that seals and common porpoise are probable predators on smolt and adult salmon in the sea and possibly responsible for the fluctuations in the salmon stock. This hypothesis was based on the fact that periods of good salmon years in the Baltic stock have followed severe ice winters in the Baltic. It is very possible that these same winters may have been harmful to the merganser populations also thus giving us one more correlation between severe winters and rich salmon periods. There are historical facts indicating that the salmon fluctuations are regular. If this leaves out to be true the regularity of severe ice winters remain to be taken into consideration.

The River Indalsälven is now blocked near the mouth by an hydroelectric plant. Its smolt production will be taken over by a salmon rearing station. The control of mergansers in this river would not affect its salmon production, but in other Swedish rivers bird control is worth undertaking.

Acknowledgement

Summary

Stomach analysis of 23 shot *Mergus merganser* and 2 *M. serrator* show that in the river Indalsälven in northern Sweden these birds feed mainly upon

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[1] Note in this connexion HUNTSMANS opinion (1948) that in the river predation is always so important that lack of food will not occur.

[2] Regard should be paid to the possible favourable effect of the merganser predating upon the miller's thumb who seems to be a food competitor and predator of salmon and trout parr.

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salmon, trout and miller's thumb, the two former species contributing at least 50 % of the food. A rough estimate indicates that the merganser population in 1954 may have consumed about 350,000 10 g salmon (or trout) parr, the mean annual smolt production of the river being estimated at about 300,000 individuals.

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On the Relation Fish Size — Food Size

By Thorolf Lindström

I. Introduction

Elton (1927) states that any one species of animal only eats food between certain limits of size, and that size of food is one of the main reasons underlying the existence of food chains. It may be assumed that the great variability of fish growth must result in fish consuming food within a rather wide size range; in fact young specimens and fish from dwarf populations of some salmonids have a tendency towards consuming food from a different trophic level (plankton Crustacea) than adults with good growth (feeding on other fish). The following study of char and zooplankton populations illustrates the size relation between predator and prey in a North Swedish lake. Such a study demands a thorough plankton investigation. The author has published a paper on the plankton from some lakes in Jämtland (1952), which partly meets this demand. Char stomach content is analysed from three of these lakes — Ånn, Ottsjön and Hottön — but Lakes Gesten and Håckren are also referred to in the discussion. In Lakes Ottsjön and Ånn char, *Salmo alpinus* L., is the dominating fish, forming more than half the fishermen's catch. Next to char, trout is the most common fish in the catches. In both lakes there are minnow, in Lake Ottsjön burbot and grayling as well. In Lakes Hottön, Gesten and Håckren there are trout, char, grayling, pike, perch, burbot and minnow, char being less abundant than in both the other lakes.

II. The Food of Adult Char

Only the stomach content is analyzed and it is assumed that digestion has not seriously affected the content by giving false proportions there between the prey species. A cursory comparison of the plankton tables (op. cit. 1952) and Table 1 gives an idea of pronounced discrepancies between lake plankton and stomach content. The seasonal change in the char food are illustrated in Fig. 1. The increasing importance of plankton in the stomachs during the summer does not quite correspond to the development in the lakes of the

Table 1. Stomach content, char, Lakes Ottsjön, Ånn and Hottön.

The locality is roughly indicated by the letters in the locality column, referring to a map on p. 119, LINDSTRÖM 1952.

Date	Locality	Gear	Totalt catch Num-ber	Total length, cm. Min.	Mean	Max.	Char with Num-ber	Volume of the stomach content, cm³
	Ottsjön							
25/4—5/5 1947		Ice fishing (rod and line)	15				0	
15/6—18/6 1946	U—V—Y and J—NOP	Net	5	28	35	50	A: 1	0.6
							C: 1	Almost empty
14/6—17/6 1947	U—V—Y and NOP	Net	14	30	37	43	0	
29/5, 12/6—16/6 1950	V—U—S—H, between L and Q	Net	24	25	35	46	C: 4	
10/7 1946		»Otter»	8	29	33	35	0	
5/7, 29/7 1950	N—O—P and U (one specimen)	»Otter» and trolling with spoon bait	27	29	32	37	A: 5	
							C: 11	
22/7, 23/7 1950	N—O—P	»Otter» and trolling with spoon bait	26	26	34	44	B: 1 C: 11	1.8 $\bar{x} = 4.0$
11/7, 15/7, 20/7 —27/7 1951	U—V—Y and NOP	»Otter» and trolling with spoon bait	43	25	35	51	A: 2 B: 1 C: 3	
8/8 1945	U	Net	2				A: 1	
19/8—20/8 1946	U and NOP	Net	12	26	34	46	A: 8	
							C: 2	
15/8, 30/8, 1950	U and NOP	Net, »otter»	3	32	34	38	A: 3	
27/9, 29/9 1946	Between F and M	Net	32	29		50	A: 2	$\bar{x} = 0.4$
	Ånn							
28/5 1946	E	Net	1		38		0	
27/5—30/5 1947	FG	Net	12				0	
8/6—13/6 1946	B—E	Net	5	32	35	39	B: 1	2.5
21/6—23/6 1947	E	Net	8	18	37	59	A: 1	1.7
13/8—14/8 1946	E	Net	15	29	38	60	A: 5	$\bar{x} = 3.6$
							C: 5	$\bar{x} = 0.6$
	Hottön							
26/9 1946	E	Net	20	33		38	A: 5	$\bar{x} = 0.6$
							B: 1 C: 2	Almost empty

The letters in the right number-column indicate: A=plankton Crustacea (or *Eurycercus*) predominate in the stomach content, B=plankton Crustacea form about half the content, C=plankton Crustacea form a minor part of the content or the stomach is almost empty, containing occasional plankton specimens.

plankton in their stomachs

The composition of the plankton part of the stomach content	
The bulk of the content	The remaining part (only groups A and B)
Bosmina	No other items
Bosmina—Daphnia—Bytotrephes	
Bosmina (3 stomachs) Chydoridae (1)	
Bosmina (1), Bytotrephes—Daphnia (3), Eurycercus (1)	Holopedium—Daphnia (1), Bosmina (1), No other items (3)
Bytotrephes (5), Bytotrephes—Daphnia (2), Holopedium—Daphnia—Bosmina—Bytotrephes (1), Eurycercus (1), One Daphnia (1), One Bytotrephes (1)	
Daphnia	Bosmina—Bytotrephes
Daphnia—Bytotrephes—Bosmina (3), Bytotrephes—Bosmina (1), Daphnia—Bosmina (1), Bytotrephes—Daphnia (1), Daphnia (2), Bytotrephes (1), One Daphnia (1), One Bosmina (1)	
Holopedium—Bosmina, (1), Holopedium—Daphnia (1)	Bytotrephes (1), Bytotrephes—Bosmina (1)
Daphnia	No other items
Unidentified (2), Daphnia (1)	Bytotrephes
Eurycercus	Bosmina—Bytotrephes (3), Holopedium—Bytotrephes (1), Bytotrephes (1), Bytotrephes—Bosmina—one Heterocope (1), One Heterocope (1), No other items (1)
Daphnia (8)	
Daphnia—Bosmina—Bytotrephes (1), Daphnia (1)	Bytotrephes—one Heterocope (2), Bytotrephes (1)
Daphnia (2), Eurycercus (1)	
Daphnia (1), Bytotrephes—Daphnia (1)	Bytotrephes (1), No other items (1)
Bosmina—Daphnia	Bytotrephes
Daphnia—Bosmina	Bytotrephes
Daphnia (4), Daphnia—Bytotrephes (1)	Bytotrephes (3), Bosmina—Bytotrephes (1), No other items (1)
Daphnia—Bytotrephes (4), Bytotrephes (1)	
Daphnia (5)	Bytotrephes (2), Bosmina—Bytotrephes (1), No other items (2)
Daphnia	Bytotrephes
Daphnia (1), Bytotrephes (1)	

Fig. 1. The seasonal trend in the char food. *Left*: the entire column=total number of stomachs; lined part of the column=number of stomachs where plankton Crustacea form more than half the content or about half the content (i.e. groups A and B in Table 1; group C includes i.a. stomachs with one plankton specimen and cannot be used for this diagram). *Right:* number of stomachs in group A and B, expressed as percentage of the total number of stomachs.

selected cladocerean species i.e. *Daphnia, Bosmina, Bytotrephes* and *Holopedium.* The abundant Bosmina plankton in June is not very much utilized by adult char (Fig. 2). The »otter»-fishing in July forms a distinct period. The char is mainly interested in emerging mayflies and caddis-flies during this period and is easy to catch with »otter» (trolling with a set of artificial flies). The »otter»-fishing may, of course, be highly selective, only selecting the part of the char population feeding on emerging insects, but »otter»-fishing is the only form of fishing or the must profitable one during this period, so it is assumed that a high proportion of the population is feeding on emerging insects. (Trolling with spoon bait only caught a few fish of those tabulated in Table 1.) In August the plankton content in the char stomachs is considerable.

A seasonal trend in the composition of the plankton content is suggested from the data in Table 1. *Bosmina* seems more important at the beginning of the summer and is later on exceeded by *Daphnia* and *Bytotrephes.* A corresponding change in the relative abundance of *Bosmina* in the pelagial compared with the abundance of *Daphnia* is illustrated by Fig. 2. The case is, however, more complicated as *Bosmina* appears in considerable swarms in the shallow littoral during the summer. (The littoral is used here as an antonym to the pelagial. The bottom regions will not be discussed in this paper.)

Turning to a discussion of the char food and the variation in lake plankton
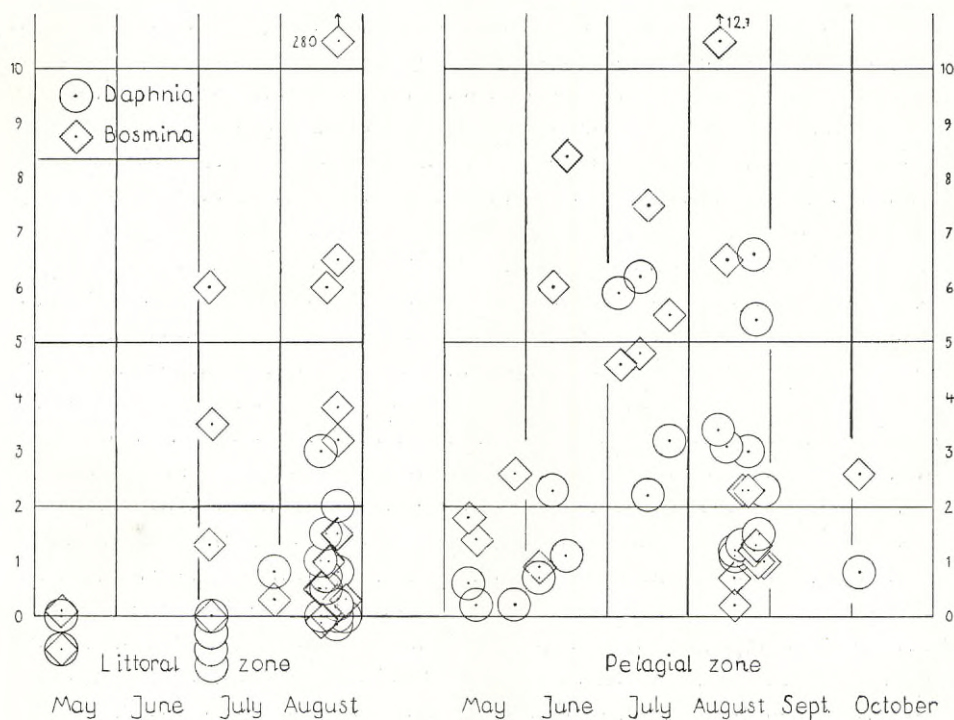
Fig. 2. The annual cycle of *Daphnia* and *Bosmina,* Lake Ottsjön. *Left:* the littoral zone. The symbols refer to averages for 5—5.3 litres, computed from the data in the plankton tables, LINDSTRÖM 1952. *Right:* the pelagial zone. The symbols refer to averages for 5—5.3 litres computed from vertical series of plankton samples from the central basin (LINDSTRÖM 1952). Samples from 2 metres below the surface are excluded as this depth was sampled only in July and August 1950—1951. This exclusion does not seriously affect the general trend in the graph.

between stations and between depths, (Fig. 3, Table 2), it can be stated that the calculation of a forage ratio necessitates either plankton sampling from the localities where the char usually forages or a plankton of uniform composition throughout the whole lake. Such a uniform plankton must be a very rare occurrence, if it exists at all. A vertical stratification of plankton is one of the most basic and frequently-studied phenomena in plankton science. There is also ample evidence of variations in horizontal distribution of plankton. The variance within a group of plankton enumerations is, moreover, always greater than one might assume if thinking in terms of normal distribution. There remains the other alternative: plankton sampling on the forage localities. Some knowledge of the short term movements of char is then desirable. A study of the char movements in Lake Ottsjön was published by the author, 1954. It indicated that an exchange of char between three, widely-spaced fishing regions does not normally occur in summer. The material

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certainly does not confirm the conclusion that those char tabulated in Table 1 in the present paper must have foraged where they were caught; they might as easily have moved in from adjacent littoral or pelagial localities. One may still tackle the problem, if the plankton samples are sufficiently close to be characteristic of all the different parts of the lakes. No doubt the actual plankton samples are far from being sufficiently numerous but they may serve for a first attempt at analysing the problems of char feeding and char habitat. In the author's plankton investigation (1952) the pelagial of Lakes Ånn, Ottsjön, and Hottön was sampled at 17 stations (763 samples) during May—October and the littoral was sampled at 26 stations during the same period (112 samples). Corresponding values for the important period July—August are: 16 stations, 471 samples in the pelagial; 22 stations, 69 samples in the littoral. The difference between years was also discussed and this and an unpublished MS (data from Lake Håckren) do not indicate differences between years of a magnitude relevant for the present discussion.

One might argue that there are one-species swarms in the lake plankton and that char starts feeding only when it meets a swarm. The variation between samples is considerable e.g. in the shallow littoral. This region is normally poor in plankton but swarms are observed now and then in middle and late summer. The swarms consist of *Bosmina* or *Polyphemus,* but certainly not of *Daphnia* or *Bytotrephes.* (Verbal comm. from Dr. STEN VALLIN, unpublished MS of NYLÉN and LINDSTRÖM 1952 p. 112—113.) The existence of *Bosmina* swarms may account for the *Bosmina* content in some of the char stomachs. *Bosmina* is not necessarily selected then, but in early summer such swarms are not observed and *Bosmina* is probably selected out of a compound plankton, containing i.a. *Cyclops* and *Diaptomus* copepodites. Adult *Daphnia, Holopedium* and *Bytotrephes* are always obtained in a compound plankton with large numbers of copepods. Table 2 and Fig. 2 show some of the characteristics of the lake plankton, and Table 2 also shows that it would be difficult to illustrate food selection, i.e. selection of Cladoceres, with the present plankton material from Lake Hottön. In this lake the cladocerean proportion of the crustacean plankton is higher than in Lakes Ottsjön

Fig. 3. Stomach content and plankton abundance in Lake Ottsjön (below) and Lakes Ånn and Hottön. Lined part of the column=number of stomachs where the plankton species (indicated below the column) enters as dominant food (Table 1, group A and B, »the bulk of the food»). White part of the column=number of stomachs where the plankton species is of minor importance (Table 1, group A and B, »the remaining part», and group C). Note: the total number of stomachs varies between months.
The lake plankton symbols refer to the percentage composition of the plankton Crustacea (nauplii excluded) tabulated in Tables 9 and 10, Lakes Ånn and Ottsjön, day samples, LINDSTRÖM 1952. Note: as the littoral is normally poor in plankton, the occurrence of a swarm affects the percentages seriously, (34 *Heterocope* 4/7 1950, 1,300 *Bosmina* 21/8 1950; 170 littoral plankton Crustacea in July totally, and 1,630 in August). [1] *Eurycercus* excluded. *Eurycercus* is not a real plankton animal.
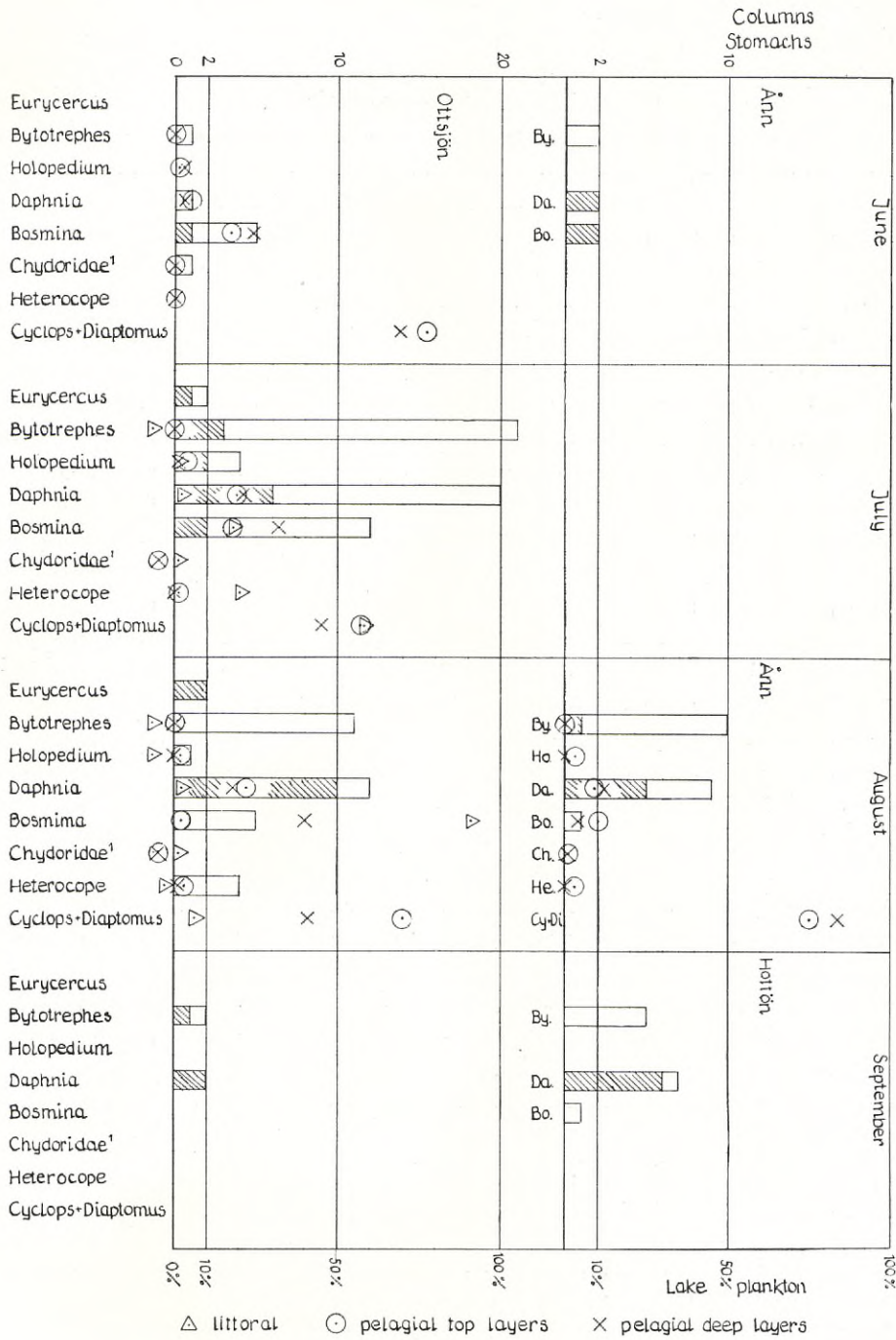
Fig. 3.

Table 2. Frequencies of plankton samples (day samples) grouped according to the percentage of the total number of plankton Crustacea made up by *Daphnia*, *Bosmina* and *Cladoceres*. (0—10, 10—20, etc. The limits included in the lower groups.) Note: nauplii are excluded from the totals in Lakes Ottsjön and Ånn.

Lake	Month	Locality	Percentage										
			0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100	
Ottsjön	June	Pelagial 0—10 m.	26	3	—	—	—	—	—	—	—	—	Daphnia
			12	9	6	2	—	—	—	—	—	—	Bosmina
			4	10	8	6	1	·—	—	—	—	—	Cladocera
	June	Pelagial 15 m.-bottom	18	—	—	—	—	—	—	—	—	—	Daphnia
			9	4	—	1	1	1	—	1	1	—	Bosmina
			3	5	3	—	3	—	1	1	2	—	Cladocera
	July	Pelagial 0—10 m.	14	16	9	7	—	2	—	—	—	—	Daphnia
			26	8	6	4	1	—	1	1	—	1	Bosmina
			5	4	9	10	9	6	—	2	1	2	Cladocera
	July	Pelagial 15 m.-bottom	10	7	7	8	5	—	—	—	—	—	Daphnia
			10	9	6	5	3	—	—	1	3	—	Bosmina
			3	1	2	1	17	2	2	4	4	1	Cladocera
	July	Littoral	11	—	1	—	—	—	—	—	—	—	Daphnia
			5	—	1	1	1	1	—	—	—	3	Bosmina
			3	—	1	1	1	1	—	1	—	4	Cladocera
	August	Pelagial 0—10 m.	43	35	23	12	9	6	3	1	—	—	Daphnia
			123	6	2	1	—	—	—	—	—	—	Bosmina
			34	26	26	18	15	7	4	2	—	—	Cladocera
	August	Pelagial 15 m.-bottom	45	17	8	3	8	4	2	1	—	—	Daphnia
			42	15	10	3	6	5	—	3	3	1	Bosmina
			19	12	13	8	4	11	6	4	6	5	Cladocera
	August	Littoral	26	2	4	3	3	—	1	1	—	—	Daphnia
			14	4	3	—	8	—	2	1	1	7	Bosmina
			2	2	2	5	4	3	6	4	1	11	Cladocera
Ånn	June—July	Pelagial	4	1	1	—	—	—	—	—	—	—	Daphnia
			4	1	—	—	—	1	—	—	—	—	Bosmina
			2	2	—	1	—	1	—	—	—	—	Cladocera
	July	Littoral	2	—	—	—	—	—	—	—	—	—	Daphnia
			—	—	—	—	1	—	—	—	1	—	Bosmina
			—	—	—	—	—	1	—	—	—	1	Cladocera
	August	Pelagial 0—10 m.	18	4	—	—	—	1	—	1	—	—	Daphnia
			19	—	1	1	—	—	1	1	1	—	Bosmina
			13	1	2	3	—	—	—	2	3	—	Cladocera
	August	Pelagial 15 m.-bottom	12	—	—	—	—	1	—	—	—	—	Daphnia
			12	1	—	—	—	—	—	—	—	—	Bosmina
			10	2	—	—	—	—	1	—	—	—	Cladocera
Hottön	June—July	Pelagial	12	5	1	3	2	1	1	1	—	—	Daphnia
			14	5	3	1	—	1	1	1	—	—	Bosmina
			9	2	3	2	2	2	1	3	1	1	Daphnia+Bosmina
	August	Littoral	4	2	—	1	—	—	—	—	—	—	Daphnia
			1	—	1	—	1	2	—	1	—	1	Bosmina
			1	—	1	—	1	—	—	1	2	1	Daphnia+Bosmina
	August	Pelagial 0—10 m.	6	8	2	4	6	——	2	5	5	1	Daphnia
			15	7	5	5	4	1	—	1	1	—	Bosmina
			2	1	2	3	2	7	3	2	7	10	Daphnia+Bosmina
	August	Pelagial 15 m.-bottom	1	7	2	6	1	4	4	5	—	2	Daphnia
			15	5	2	4	4	1	1	—	—	—	Bosmina
			1	1	4	2	1	3	2	5	7	6	Daphnia+Bosmina

Table 3. Numerical data, illustrating the char stomach content, August 1946 (1—9) and July, 22nd and 23rd, 1950 (10—20). Only the consumed plankton Crustacea are considered.

	Counted part (%) of the total plankton content	Numbers of plankton Crustacea				Lake
		Daphnia	Bytotrephes	Bosmina	Heterocope	
1	—	326	27	—	—	Ånn
2	3	217	5	—	—	»
3	3	210	+	—	—	»
4	50	602	13	2	1	Ottsjön
5	50	22	1	2	—	»
6	10	877	4	1	—	»
7	17	600	4	—	—	»
8	50	659	3	2	—	»
9	100	85	—-	—	—	»
10	100	—	146	1	—	»
11	100	56	2	4	—	»
12	100	70	41	8	—	»
13	100	—	3	—	—	»
14	100	11	6	1	—	»
15	100	24	—	—	—	»
16	100	370	29	29	—	»
17	100	14	—	—	—	»
18	100	1	2	—	—	»
19	100	1	—	—	—	»
20	100	—	—	1	—	»

and Ånn. In order to emphasize this fact the author has included nauplii in the totals only when calculating the percentage values in Table 2 for Lake Hottön. As it is rather doubtful if nauplii can serve as food for adult char, the nauplii are excluded from the totals when calculating the percentages for Lakes Ottsjön and Ånn. Those rare cases when the percentages for the pelagial samples from Lakes Ottsjön and Ånn exceed 80 refer almost exclusively to *Bosmina* and aggregations of young *Daphnia* females and *Daphnia* males near the bottom. Young *Daphnia* females and *Daphnia* males are very seldom observed in the char stomachs. The *Daphnia* in the stomach content consisted of adult *Daphnia* females, which are concentrated in the layer two metres below the surface in August. The selection of *Daphnia* seems more pronounced than that of *Bosmina* (Fig. 3).

Bytotrephes attracts special interest as char food and some information about this animal is obtained. Only 14 specimens are recorded from 875 samples from the Lakes Hottön, Ottsjön, and Ånn. One may presume that this big plankton species can see the sampler and thus escape now and then, but considering the technique employed (op. cit. p. 72) one may safely state that the *Bytotrephes* is a rare animal compared with *Cyclops, Bosmina, Daphnia,* and *Diaptomus.* The char must hunt through a considerable volume of water to select the number of *Bytotrephes* recorded in some stomachs (Table 3). Out of 17 *Bytotrephes* recorded in the plankton tables (op. cit.),

one animal was caught at a depth of 15 metres, all the others were caught higher up in the pelagial (Cf. HUITFELDT-KAAS 1906).

A *statistical* analysis is not attempted in this paper. Data on stomach content are always approximate. The largest plankton species may escape the plankton sampler (cf. discussion about *Bytotrephes*). Moreover, if char starts feeding on plankton only when it meets a swarm, an analysis of variance including all the plankton samples is not relevant.

III. The Food of Char Fry

This report is based on food analyses of fry from Lake Kallsjön (LINDSTRÖM, 1952, Map, p. 117). The eggs were kept in a hatchery during the winter and hatched in March 1947. The bulk of the fry were then kept in a trough, where the temperature in April reached 5° C and in May 15° C. The temperature during winter and spring did not strictly follow the temperature on the spawning places and habitats of fry in the lakes. Smaller quantities were transported at intervals to aquaria supplied with food and it was thus established that they could start eating in late April—early May. The bulk of the fry were kept in the trough and received practically no food until early June, as shown by filtering the entering water and dissecting the digestive tract of 109 fry. Their yolk sacs were resorbed towards the end of May and a heavy mortality started to occur in June, when the fry were very thin. The fry were almost entirely interested in moving food items only, as shown i.a. by experiments, when 35 fry were kept without plankton in aquaria with algae covering the stones, higher plants and glass walls. The digestive tracts of these fry were empty or almost empty. Experiments when the char fry were feeding on pike fry were more elucidating. The char fry followed (and swallowed) pike fry when these dashed forward, but the char fry completely lost their interest in the pike fry when these rested motionless in between whiles. A part of the char fry were kept in aquaria supplied with pond plankton during the period April 26th—June 13th. Copepods dominated the pond plankton in the beginning, Cladoceres later on. Out of 31 fry dissected the majority had eaten Cladoceres. 14 had eaten Copepods (copepodites or adults) in varying proportions with other food items. The experiment does not permit any conclusions to be drawn as to the selection of different plankton species.

Char fry from lakes are hard to obtain. Two fry were caught from Lakes Gesten and Ånn on the 4th and 7th of June 1955. Their ontogenetic development was more advanced than that of the fry from the experiment in June 1947 judging by the morphology of the digestive tract, the resorbed yolk sac, the presence of parr marks and their length (26 $^1/_2$ and 26 mm for the fry caught 1955). Their stomachs contained small insect larvae (fry from Lake Gesten) and plankton (fry from Lake Ånn: about 75 *Cyclops* copepodites and 4 *Bosmina*).

IV. Is the Strength of the Year-classes of Char Determined by the Plankton Abundance in Spring?

In the aquarium experiments it is shown that the fry may consume food items of very different kinds as long as the items are moving. They ate i.a. Copepods, which is important as the Copepods dominate the winter and spring plankton in the lakes. The investigations made by RUNNSTRÖM (1946) and the state of the two wild fry reported in this paper indicate that char fry starts feeding sometime between March and May. The plankton on the spawning places in Lakes Gesten and Hottön was samples 29/3 1946 and 8/3 1950: the 61 litres filtered contained only three nauplii (see LINDSTRÖM, 1952, Table 9 and Maps on p. 119—120, stations D and E). 53 litres sampled from a spawning place in Lake Håckren 2/6 1955 contained only six nauplii, three *Bosmina,* two rotifers and one *Daphnia* (cf. Map op. cit. p. 120, approximately station B). Giving every possible credit to the fact that char fry can survive lack of food in their vicinity as long as the yolk sac is not quite resorbed, it seems improbable that plankton Crustacea form the main food of the char fry in their first spring in Lakes Håckren and Gesten, where the pelagial region too is poor in plankton in the winter and spring. In the other lakes the spawning places were not tested for plankton (Ånn and Ottsjön) and the fry may have access to a pelagial with more abundant plankton (Hottön, Ånn and Ottsjön). Further investigations are thus necessary.

V. Indications Regarding the Habitat of Adult Char

Bytotrephes and adult *Daphnia* females form a considerable part of the plankton in the stomach content of char. In the lakes they are concentrated in the top layers in July and August, and 2 metres below the surface in August respectively. It is true that adult *Daphnia* females may be found in most parts of the pelagial but as the density of *Daphnia* decides whether or not it is consumed by char, the facts suggest that char inhabits the top layers of the lakes when feeding on plankton (other char populations are known to inhabit deep layers in other lakes NERESHEIMER 1937, MÄÄR 1949). Feeding on plankton Crustacea in the top layers of the lakes in August thus succeeds feeding on emerging insects in July in the annual cycle.

VI. Food Selection of Char

Aquarium observations show that fish do not generally filter the food from the lake water (BATTLE et alii 1936, herring; WAGLER 1941, whitefish; FABRICIUS 1953, char). From this fact one can infer that fish food will probably

constitute a selection of certain plankton species — though not necessarily due to an active choice on the part of the fish. For an analysis of the selective mechanism it would be desirable if one could distinguish between the particles that are observed and that could be caught by the fish and the lesser group that functions as stimuli and releases prey-catching actions. An analysis also demands a definition of the availability of a food particle, taking into account not only its abundance but also its visibility, activity etc. (RICKER 1937, ALLEN 1941 absolute availability). The application of this term gives rise to the question: what is »received» by the sense organs of fish? RICKER paid special attention to a case where fingerlings of sockeye salmon made divergent selections of food from a uniform environment (a small cage), and this is obviously the way to proceed, but cage experiments with char have not so far succeeded. A full discussion of the selective mechanism demands a new set of definitions but this must await further studies.

There are indications of food selection in the present material from Lakes Ottsjön and Ånn (Ch. II). It is possible that *Diaptomus* jumps too vigorously to be caught by the char. The activity of different plankton species may be illustrated by experiments with a siphon (NAUMANN 1921) and with plankton pumps (LANGFORD 1953). One may arrange the plankton species in series, going from animals that cannot possibly avoid being captured by the current to animals well able to retain their places: *Daphnia, Diaphanosoma, Bosmina, Polyphemus* (NAUMANN's data) or nauplii, *Cyclops, Daphnia, Diaptomus, Diaphanosoma* (LANGFORD's data). The details of these series may be criticized but knowing that trout fry (MOTTRAM 1931), sockeye fingerlings (RICKER 1937) whitefish fry from Lake Uddjaur and char fry (the author's observations) consume *Cyclops* adults and/or copepodites, it is hard to believe that adult char does not observe or cannot catch *Cyclops*. It is far more likely that the sight of *Cyclops* releases a prey-catching action in the fry, but does not release this action in adult char when feeding on plankton of the composition recorded from the Jämtland lakes. Most kinds of plankton Crustacea can serve as food for Salmonids: *Heterocope* is the main food of whitefish in spring and autumn in Lake of Geneva according to ELSTER (1944, p. 224), *Polyphemus* and *Diaphanosoma* is consumed by salmon fry in a rearing pond according to GRIMÅS et alii (1954). Nevertheless adult char selects a) Cladoceres and b) large and bulky Crustacean as *Bytotrephes*, adult *Daphnia* females and *Heterocope* when feeding on the summer plankton of the Jämtland lakes (the only Copepods obtained in the stomachs were four *Heterocope*, the largest of the Copepods). Only one quality of the situation releasing a prey-catching action in char will be discussed: the size of the prey.

The char diet corresponds closely to that reported by BRUNDIN (1942), FROST (1946, 1951) SCHINDLER (1950) and NILSSON (this volume), except for FROST reporting that the »giant» *Leptodora* is included in the main food. There are studies of the diet of Salmonids showing or suggesting selection

of Cladoceres and large plankton Crustacea (whitefish: BOHMANN et alii 1939, ELSTER 1944; char: FROST 1946, NILSSON 1955) and the similarity between the selection made by char and that made by whitefish is pronounced. Other investigations only suggest a selection of Cladoceres (SOUTHERN 1932, trout; SCHINDLER 1950, char), but do not exclude the possibility of a selection with regard to food size also being in operation.

A great many observations show that there is an approximate correlation between the size of the food (plankton Crustacean — bottom animals — prey fish) and the size of the fish. The correlation is valid both for differences in fish size within a population and for differences between populations in the average individual size, »dwarf» populations often feeding on plankton (DAHL 1917, trout; HUITFELDT KAAS 1927, trout; SOUTHERN 1932, trout; RICKER 1937, sockeye salmon; NERESHEIMER 1937, char; ALLEN 1941, salmon; WAGLER 1941, whitefish; ELSTER 1944, whitefish; ALM 1946, perch; SCHINDLER 1950, char; NILSSON 1955, char; LINDSTRÖM 1955, whitefish). The growth of fish is controlled by several factors and there is ample evidence showing the importance of the amount of food per individual fish. It is possible that those habitats where fish consume plankton are often overcrowded or that the fish shoals possible cause a temporary decrease in plankton density (ELSTER 1944, p. 292). These hypotheses cannot, however, account for the fact that fish select large food items when feeding on bottom animals (NILSSON 1955) or that adult fish select large plankton Crustacea, while fry and young fish consume smaller crustacean plankton.

An old theory already presented e.g. by DAHL 1917 accounts for all the known facts: the size or rather the nutritive value of the food items has an influence on the growth of the fish. The size may be important only as a quality of the stimulus releasing a prey-catching action. As far as plankton Crustacea are concerned, it is assumed that size is correlated to the nutritive value in an approximate manner.

Summary

Some interrelations between char and plankton Crustacea are studied.

The material suggests that the plankton in some lakes is too scarce to be the main food of char fry when the fry start feeding in late winter and spring.

Aquarium experiments show that char fry can consume food items of very different kinds as long as the items are moving.

The food of adult char from some lakes is studied and the lake plankton is analysed (samples: 5—5.3 litres). Attention is paid to the seasonal variation and the variation between depths and between stations in plankton abundance and plankton composition. It is not possible to compute a forage ratio and to analyse this material statistically. Nevertheless the material suggests that the

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adult char selects a) Cladoceres and b) large types of plankton Crustacea (*Bytotrephes,* adult *Daphnia* females, *Bosmina, Heterocope*). The mechanism and the significance of food selection is discussed.

Certain facts indicate that char inhabits the top layers of the lakes studied when feeding on plankton.

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Produktionsbiologische Untersuchungen in Nord-schwedischen Fliessgewässern

Teil: 3. Die Bedeutung der Seen und Stillwasserzonen für die Produktion in Fliessgewässern

Von Karl Müller

Vorwort

In seiner sehr gründlichen und eingehenden Untersuchung über die Statik und Dynamik einer Biozönose unterhalb eines Teichausflusses konnte Knöpp (1952) zeigen, dass die Bachfauna qualitativ wie quantitativ durch die Lebensabläufe im Teich geprägt wird: Der vom Autor mitgeteilte dominierende Prozentsatz »passiver Ernährer» konnte nur in Abhängigkeit von dem vorgelagerten Teich auftreten. Dieser an einem kleinen Bach in Südwest-Deutschland beschriebene Vorgang deutet allgemeingültig einen Prozess an, der in der Limnologie fliessender Gewässer bisher wenig Beachtung fand.

Unsere im Gebiet des Lule-Älvs in Durchführung befindlichen Untersuchungen lassen erkennen, dass auch hier den in den Flussverlauf eingeschalteten Seen und Stillwasserzonen eine entscheidende Bedeutung für Vorkommen, Menge und Verbreitung der Bodenfauna zukommt. Damit ergibt sich zugleich auch die Bedeutung dieser Seen für die fischereiliche Produktion. Es lässt sich ausserdem zeigen, wie ein Eingriff in die Wechselbeziehung See: Fluss (Kraftwerksbau) die Ausbildung natürlicher Ausflussbiozönosen stört oder gar in ihrer Entwicklung ganz unterdrückt.

1. Das Untersuchungsgebiet

Eine Übersicht über das Flussystem des Lule-Älvs gibt die Abb. 1. Das Einzugsgebiet des Flusses erstreckt sich von 68° 10′ N bis 65° 30′ N in SO Richtung. Er mündet in den Bottnischen Meerbusen bei der Stadt Luleå. Die Hauptwasserzuführer sind der Stora Lule Älv, Lilla Lule Älv und der in diesen mündende Pärl Älv. Um einen Überblick über die Grösse der hier behandelten Wasserflächen und die Zahl der im Einzugsgebiet befindlichen

Tab. 1.

Flussystem	Flusslänge km	Einzugsgebiet km^2	Seen im Flussystem	
			Anzahl	Fläche (km^2)
St. Lule Älv	450,5	25.245	4.388	1.959,1
Vietasjokk	112,4	2.371	411	284,7
L. Lule Älv	228,2	9.607	1.638	614,9
Pärl Älv	134,6	2.250	459	155,9
Black Älv	107,0	2.456	185	75,1

Seen zu geben, sind im Folgenden einige hydrographische Daten aufgeführt (nach WERSÉN 1925).

Die Hauptwasserquellen des Lilla und Stora Älvs sind Schnee- und Gletscherschmelzwässer. Dies bedingt einen gänzlich anderen Gewässercharakter als wir ihn aus der Nadelwaldregion des gleichen Gebietes mitgeteilt haben (MÜLLER 1954). Während in der Waldregion das Vorkommen einer ausgeprägten Forellenregion als Ausnahmeerscheinung angesehen werden muss, wiederholt sich hier im Hauptfluss und in den in der Gebirgsregion liegenden Nebenflüssen die gleiche regionale Zonierung, wie sie für verschiedene mitteleuropäische, englische und nordamerikanische Flussysteme bekannt ist. Der wesentliche Unterschied zu der mir bekannten Zonierung in Mitteleuropa liegt darin, dass die dortigen Flüsse (z.B. im deutschen Mittelgebirge: Rhön, Vogelsberg, Weserbergland) auf relative kurze Strecken recht scharf begrenzte Bereiche der Salmonidenregion aufweisen (Vergl. ILLIES, 1953, p. 14, Abb. 1). Bei einer Gesamtflusslänge der vom zitierten Autor behandelten Fulda von 220 km fallen nur 20 km auf die Teile der Salmonidenregion.

Im Stora Lule Älv dagegen müssen wir bei einer Gesamtlänge von 450,5 km ca 320 km zur Salmonidenregion rechnen (Zusammenfluss mit Lilla Lule Älv bei Porsi). Da die Temperatur der wesentliche Faktor für eine Abgrenzung der einzelnen Zonen ist, d.h. das Auftreten einzelner Arten und Biozönosen bedingt, erklärt sich die Grösse der Salmonidenregion nordischer Ströme aus der niedrigen Mitteltemperatur der hiesigen Gewässer. Man wird sicher von Süd nach Nord gehend in Skandinavien alle Übergangsformen von kurzer Salmonidenregion bis zu der extrem langen Salmonidenregion des Hohen Nordens feststellen können.

Bei der Länge der Ausdehnung der Salmonidenregion infolge der nur sehr allmählich sich ändernden Temperaturamplitude ist zu erwarten, dass sich ihre Abgrenzung gegenüber der folgenden Zone — der Barbenregion — schwierig gestaltet. Diese Abgrenzung wird aber andererseits dadurch erleichtert, dass die in den Flussverlauf eingeschalteten Seen eine abrupte Änderung des jährlichen Temperaturverlaufes verursachen und so selbst zur Zonengrenze werden. Ein Blick auf die Höhenlage der einzelnen Seen zeigt, dass im Vertikalprofil diese Seen terassenförmig angeordnet sind und zwi-
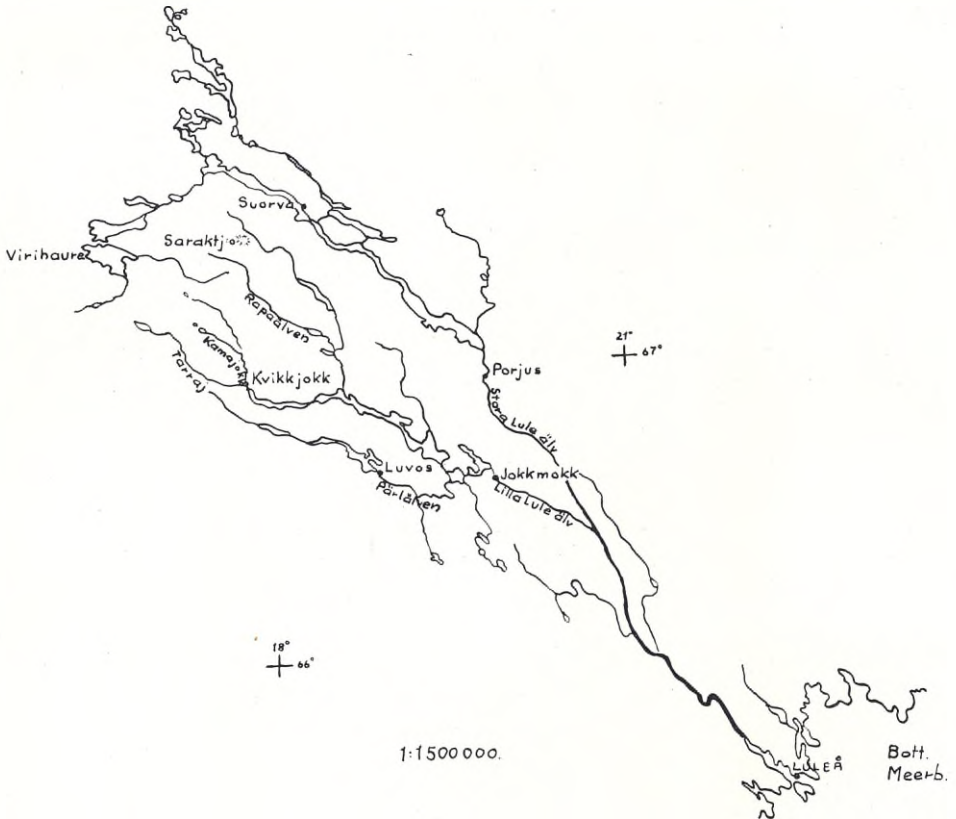
Abb.: 1. Übersicht über das Flusssystem des Stora und Lilla Luleälv.

Fig. 1. Survey of the river system of Stora and Lilla Luleälv.

schen ihnen mehr oder weniger lange Stromschnellenbereiche (»Forse») ein-geschaltet sind.

Unterhalb der marinen Grenze, bei ca 200 m Meereshöhe, treten solche Seen im Flussgebiet nicht mehr auf. Auch hier sind jedoch die Stromschnellen-bereiche von ausgedehnten Stillwasserzonen (»Sel») unterbrochen, in denen sich nun die Temperatur- und Strömungs-Bedingungen einer Barbenregion einstellen. (Die Barbe selbst — der Charakterfisch dieser Region in Mittel-europa — fehlt allerdings infolge seiner weiter südlich liegenden Verbrei-tungsgrenze!) Die Abb. 2 zeigt schematisch den geschilderten Verlauf eines typischen Stromes im hiesigen Gebiet auf einem geographischen Querschnitt durch Nordschweden. Überall in den schnellfliessenden Bereichen treffen wir auf die Salmonidenregion, oberhalb der marinen Grenze werden diese durch *Coregonus*-Seen unterbrochen, unterhalb dieser Linie aber durch die der mitteleuropäischen Barbenregion ähnelnden Stillwasserergebiete (Sel).
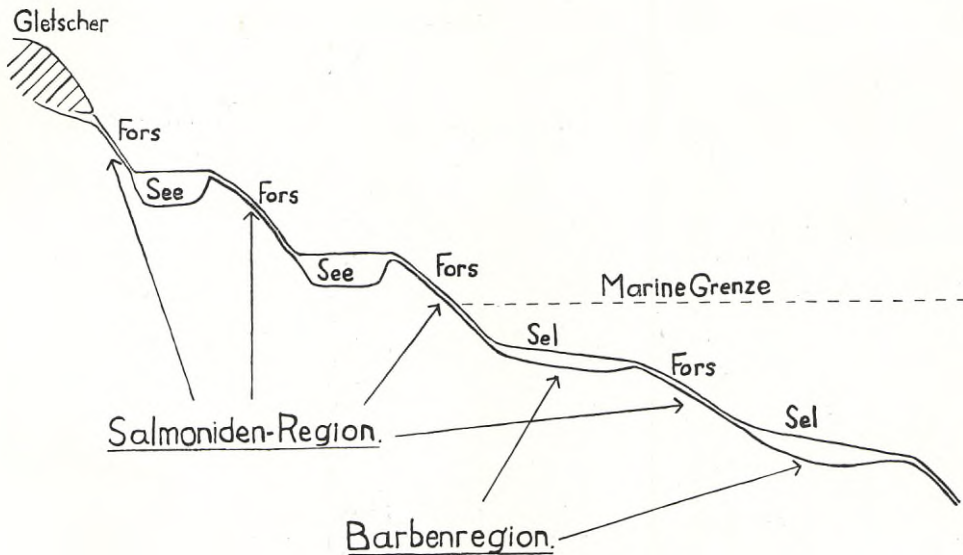
Abb.: 2. Schematische Darstellung des Verlaufes eines skandinavischen Stromes.
(Fors=Stromschnelle, Sel=Stillwasserzone.)

Fig. 2. Schematic representation of the course of a Scandinavian river.
(Fors=rapid, sel=zone of calm water.)

2. Untersuchungen und Beobachtungen über den Einfluss von Seen und Stillvasserzonen auf den qualitativen und quantitativen Bestand der Bodenfauna im Stromschnellenbereich

Es sei zunächst die Besiedlungsdichte an Benthosorganismen in einem für Schweden »normalen« — d.h. von Stillwasserzonen unterbrochenen — und in einem ohne See-Durchfluss direkt von der Quelle abfliessenden Flusse verglichen.

Abb. 3 zeigt die gefundenen Werte (in mg/qm/lo) in zwei solchen physiographisch vergleichbaren Fliessgewässern Mittelschwedens, dem Hovermo-Ån und dem Tandsjö-Ån (Provinz Jämtland). Es zeigt sich, dass der Tandsjö-Ån nach seinem Durchfluss durch den See Tandsjö fast die zehnfache Benthos-Masse aufweist wie der seenfreie Hovermo-Ån.

Die einzelnen Organismengruppen, die diese Massen bilden, wurden unterteilt in solche, die sich »aktiv« ernähren (d.h. auf dem Untergrund auf Nahrungssuche umherkriechen) und solche, die eine »passive« Ernährungsweise besitzen (d.h. am Untergrund fixiert sind und mithilfe von Reusenapparaten oder Fangnetzen die von der Strömung herbeigeführte Nahrung einfangen und aufnehmen).

Passive Ernährer sind dabei vor allem: *Spongia,* netzbauende Trichopteren (Gattung *Hydropsyche, Neureclipsis, Plectrocnemia*) und die Larven der Simuliiden.

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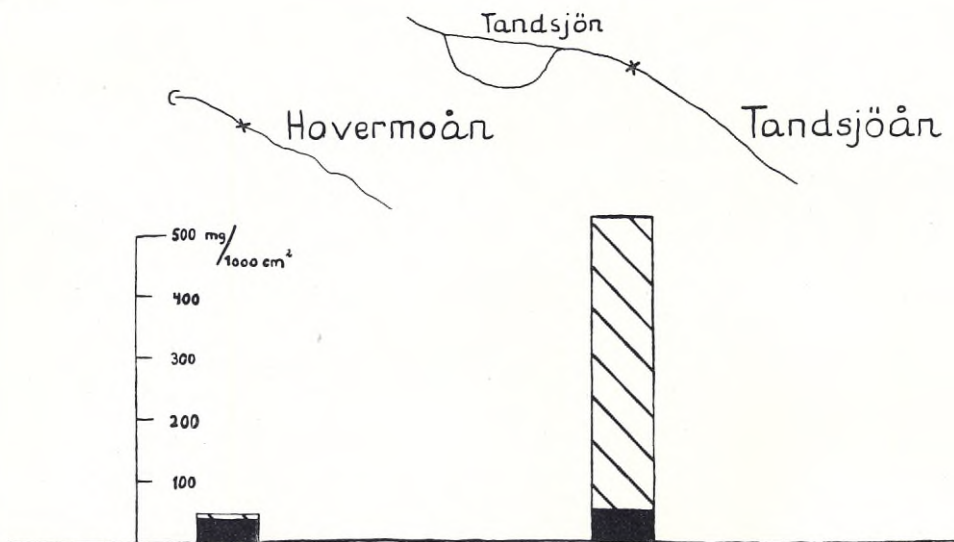
Abb.: 3. Die Verteilung »aktiver und passiver Ernährer« in natürlichen Flusssystemen mit (Tandsjöån) und ohne (Hovermoån) Seeneinfluss.

Fig. 3. The distribution of »active and passive feeders« in natural river systems with (Tandsjöån) and without (Hovermoån) influence of lake fauna.

Als aktive Ernährer dürfen alle übrigen Gruppen, also vor allem Ephemeropteren, Plecopteren, räuberische und gehäusetragende Trichopteren, Coleopteren und Chironomiden angesehen werden.

Bei einer solchen Unterteilung der Benthosformen des Flusses zeigt sich eindeutig (s. Abb. 3), dass der ausserordentliche Mengenzuwachs im Tandsjö-Ån ausschliesslich die Gruppe der passiven Ernährer betrifft. Gibt uns die Besiedlung des Hovermo-Ån das normale Bild einer Fliesswasserbiozönose wieder, bei der neben einem hohen Prozentsatz von aktiven Ernährern eine geringe Menge von Organismen auftritt, welche von der organischen Flussdrift (s. MÜLLER 1953) leben, so tritt unterhalb eines Seedurchflusses infolge der durch ihn bedingten organischen Seendrift eine so starke Eutrophierung der Wassermassen ein, dass die Formen, welche das vorbeiströmende Wasser filtrieren, in enormen Mengen existieren können.

Es sei noch erwähnt, dass das Besiedlungsbild unterhalb von Seendurchflüssen in Abhängigkeit von der Jahreszeit variiert, wie dies bei der jahreszeitlich verschiedenen Flugperiode der einzelnen Komponenten nicht anders zu erwarten ist. In unseren Untersuchungen zeigte sich stets ein hohes Frühjahrsmaximum, das im Wesentlichen von *Simulium* gebildet wird. Nach der Hauptflugzeit dieser Tiere folgt eine Periode geringerer Besiedlungsdichte: Chironomiden (*Orthocladiinae*) treten mehr in den Vordergrund. Schon Ende Juli beginnt dann erneut ein merkliches Anwachsen der Besiedlungszahlen,

Tab. 2: Passive und aktive Ernährer in verschiedenen Stromschnellen-
bereichen des Lule Älvs.

Ort	Passiv (mg/qm/lo)	Aktiv (mg/pm/lo)
Louvos	867,5	228,9
Purkijaurefors	362,9	80,5
Kaitumfors u. Akatjfallet ..	348,0	113,2
Porsifors	291,9	70,5
Edefors	167,0	60,3
Vittjärvfors	192,0	60,4

das durch das Heranwachsen der verschiedenen netzbauenden Trichopteren-
arten bedingt ist.

Wenden wir uns nun unserem Hauptuntersuchungsgebiet, dem Lule Älv
und seinen Zuflüssen, zu. Aus den zahlreichen aus diesem Gebiet vorliegenden
Befunden seien die herausgegriffen, welche auf dem Wege Pärl Älv—Lilla
Lule Älv—Lule Älv hintereinanderliegende Stromschnellenbereiche betreffen.

Die Abb. 4 stellt diese Befunde graphisch dar und gibt ausserdem einen
geographischen Überblick über die Lage der Sammelstellen und ein halb-
schematisches Querprofil mit Angabe der Höhenlagen.

Der bereits beim Tandsjö-Ånn konstatierte Effekt (s. Abb. 3) zeigt sich
wiederum mit aller Deutlichkeit: die Zahl der passiven Ernährer überwiegt
bei weitem die der aktiven.

Eine ins einzelne gehende Diskussion der Ergebnisse ergibt dabei weit-
gehende Rückschlüsse auf die Abhängigkeit dieser Biozönosen von den vor-
gelagerten Stillwasserzonen. Die ausserordentliche Höhe der Besiedlungswerte
unterhalb des Karats-Sees dürfte ein Ausdruck für die besondere Grösse dieses
Gewässers sein, die sich in einer besonders grossen Produktion und demzu-
folge in einer erheblichen Seendrift niederschlägt. Dabei ist zu bemerken, dass
dieser See trotz seiner Höhenlage nicht von Gletscherschmelzwassern gespeist
wird, sondern sein Einzugsgebiet unterhalb der Eisgrenze hat. Dadurch wird
seine Temperaturkurve für die Produktion wesentlich günstiger als etwa die
des Torneträsk. Die Werte am Purkijaurefors sind demgegenüber deutlich
gesenkt. Die Seendrift des Karats-Sees ist also von den Driftfressern bereits
verbraucht und nur die infolge der geringeren Grösse des Purkijaure-Sees
verminderte Seendrift aus diesem steht den passiven Ernährern im Purki-
jaurefors zur Verfügung. Nach dem Durchfluss durch den Vaikijaure-See
(grössere Oberfläche), nimmt die Zahl der Passiven wieder etwas zu, um nun
in den sich anschliessenden seenfreien Teilen des Lule Älv (Porsifors, Ede-
fors) beständig abzusinken. Dieser Prozess wird im Anschluss an ein ausge-
dehntes Sel im Lule-Unterlauf unterbrochen: bei Vittjärvsfors ist die Zahl
der Passiven wiederum etwas angestiegen. Bei grösserer Ausdehnung können
also auch »Sel« einen see-ähnlichen Eutrophierungseffekt auf die Benthos-
fauna ausüben.

Betrachten wir die aktiven Ernährer, so fällt die erstaunliche Gleichmässigkeit auf, mit der sie an den verschiedenen Untersuchungsstellen mit ca 100 mg/qm/lo auftreten. Nur an der ersten Probenstelle (Louvos) ist auch ihre Zahl deutlich angestiegen. Dies dürfte darauf beruhen, dass die gerade dort in erheblichen Mengen auftretenden Driftfresser (vor allem *Simulium*) auch einen Mengenanstieg ihrer natürlichen Feinde unter den Benthosbesiedlern (*Cardiocladius, Rhyacophila, Perlodinae*) zur Folge hat.

Der im übrigen fast gleichbleibende Status bei den Aktiven ist den Ephemeropterenlarven zuzuschreiben, die stets in gewisser Anzahl im Flusse vorkommen (bei mangelnder organischer Seendrift sogar in hohem Prozentsatz der Gesamtbesiedlung) und die als Diatomeenbewuchs-Fresser von der Eutrophierung der Fliesswasserzonen durch die Seendrift unbeeinflusst bleiben. Gewisse Schwankungen in der Menge der Aktiven gehen ausserdem zu Lasten der Mollusken (*Limnaea peregra*), deren örtlich sehr verschiedenes, aber von der Seendrift unbeeinflusstes Auftreten das Gewicht dieser Gruppe erheblich beeinflussen kann.

Es erhebt sich bei diesen Überlegungen die Frage, in welcher Entfernung von einem See der Einfluss der organischen Seendrift spürbar ist. Dies ist in erster Linie natürlich abhängig von der Grösse und Fruchtbarkeit des vorgelagerten Sees. Es ist aber auch bedingt durch die Länge und Ausbildung des Stromschnellenbereiches unterhalb des Sees. Die an einem kleinen Bach des Waldgebietes dargestellte Seeausflussbiozönose (Vergl. MÜLLER 1954, p. 90, Abb. 5) zeigte, dass in Abhängigkeit vom Gefälle bestimmte Formen mit passiver Ernährungsweise exclusiv auftreten. Dies wiederholt sich in gleicher Weise bei grösseren Flüssen.

Das beste Beispiel dafür ist ein Vergleich zwischen dem Seenausfluss des Sees Vaikijaure (Akatjfallet) und dem Karats-Sees (Louvos). Im ersteren ist nur die »Ausflusszone I» gegeben, d.h. der Fluss tritt mit starken Gefälle aus dem See und nur die robusten Larven von *Hydropsyche* spec. finden eine Kolonisationsmöglichkeit. Umgekehrt sind die Verhältnisse im Karats-See. Hier verlässt der Pärl Älv den See mit höchstens 0,60—0,80 m/sec. Die Folge davon ist ein Massenauftreten von *Neureclipsis bimaculata*. Ein nach etwa 1 km eintretendes stärkeres Gefälle (oberhalb des Sees Piertinjaure) schaltet dann die *Neureclipsis*-Besiedlung fast völlig aus und auch hier treten *Hydropsyche*-larven an ihre Stelle.

3. Die Stromschnellen, speziell die Seeausflüsse, als Produktions- und Reproduktionsbereiche innerhalb des Flussystems

Wie wir im vorigen Kapitel zeigen konnten, besteht unzweifelhaft ein starker Einfluss der Seen auf die unterhalb gelegenen Gebiete der sie durchfliessenden Flüsse. Dieser Einfluss ist naturgemäss in Seenähe am grössten und
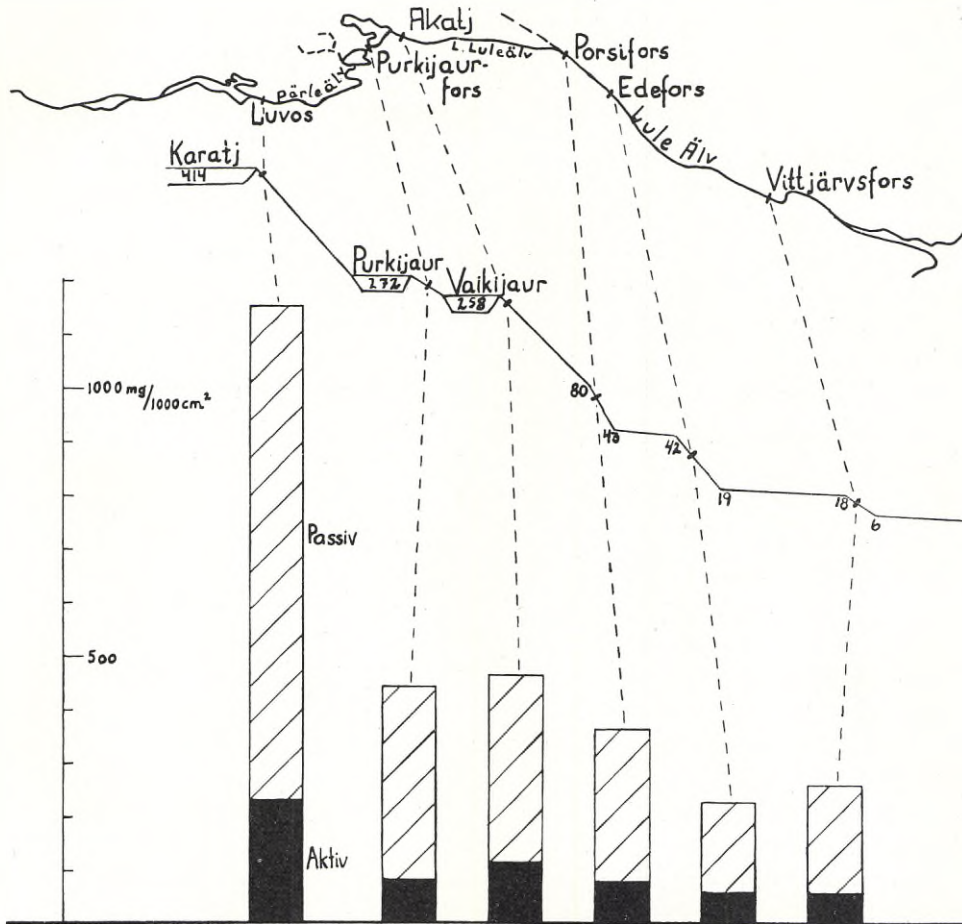
Abb.: 4. Der Mengenanteil »aktiver und passiver Ernährer« des Benthos in verschiedenen Stromschnellen des Luleälvsystems. (Ziffernangaben entsprechen Höhe über N.N.)

Fig. 4. The relative quantity of »active and passive feeders» in the bentic fauna of different rapids of the Luleälv system. (The numbers indicate the height above sea-level.)

nimmt allmählich ab. Es ist weiterhin naheliegend zu vermuten, dass diese Bereiche wegen ihrer hohen »Capacité biogenique» gute Lebensbedingungen für die Fische bieten und von diesen sowohl als Aufwuchsplätze wie auch als Laichplätze benutzt werden.

Beides ist uns aus der Jahrhunderte alten Praxis der Fischer bekannt. Unterhalb unserer Seen liegen die besten Fangplätze während des ganzen Jahres, speziell bei Beginn der Laichzeit der Salmoniden (*Salmo salar, Salmo trutta, Thymallus thymallus*). Die Sportfischerei konzentriert sich vorherrschend auf die Bereiche unterhalb der Seen Saggat (Njavefors), Skalka (Björkholmfors), Randijaure (Purkijaurefors), Vaikijaure (Akatjfallet, Kaitumfors),

Tab. 3.

Bodenfauna	Drift	Darminhalt
Heptagenia	*Diatomeae*	*Diatomeae*
Isoperla	*Rotatoria*	*Rotatoria*
Baetis	Nauplien	Nauplien

Peuraure (Lillselfors), Karats (Forse zwischen Karats und Piertinjaure). Zeigt hier bereits die praktische Erfahrung die höchsten Erträge, so lassen sich diese Tatsachen voll durch unsere Bonitätsuntersuchungen bestätigen. In dem Umstand, dass besonders die Salmoniden zur Laichzeit diese Bereiche aufsuchen, erkennen wir zwei biologische Prozesse. Einmal ist die Laichwanderung ein Ausdruck des »Besiedlungskreislaufes« (vergl. MÜLLER 1953, p. 142 ff.): der erwachsene, laichreife Fisch wandert flussaufwärts, weil er im Gegensatz zu den Jugendformen in der Lage ist, die Strömung zu überwinden. Die Laichablage erfolgt weit oben, und vom Punkte der Eiablage verteilt sich der Nachwuchs in Strömungsrichtung.

Wir erklärten aber schon in der oben zitierten Arbeit, dass noch »favourable conditions of growth for the young fishes in the higher reaches of the stream« hinzukommen. Diese verbesserten Aufwuchsbedingungen sind tatsächlich in starkem Umfang im Bereich unterhalb der Seen gegeben — für viele Fischlarven treten sie nach den Untersuchungen des Jahres 1954 sogar nur dort auf.

Einige Beobachtungen über Verhalten und Nahrungsaufnahme von *Salmo trutta* mögen dies erläutern. Die Beobachtungen erfolgten am 12.6. und 18.7. 1954 im Akatjfallet unterhalb des Sees Vaikijaure.

(12.6.1954): In einem Seitenarm des Seeausflusses (Strömung ca 40—60 cm/sec, durchschnittliche Wassertiefe 20—40 cm) bilden sich zwischen mittelgrossem Steinmaterial kleine Kolke mit Kiesablagerungen am Boden. In Schwärmen von 5—10 Fischen konnten hier *Phoxinus laevis* und *Salmo trutta* beobachtet werden. Die Forellen waren frisch geschlüpft (1,8—2,4 cm Länge) und hatten den Dottersack ganz oder doch fast vollständig resorbiert. Die Fische standen im Strom und es war deutlich zu bemerken, dass sie gelegentlich gegen den Strom vorstiessen um Nahrungspartikel aufzunehmen. Die Fische standen dabei weit über dem Boden und die Nahrungsaufnahme erfolgte nicht am Boden. Nach halbstündiger Beobachtung wurden 5 Fische gefangen. Die Besiedlung des Bodens, die Drift (Planktonnetz für 5 Min. in die Strömung und der Mageninhalt der Fische wurden untersucht. Das Ergebnis zeigt Tabelle 3.

(18.7.1954): Am gleichen Fangplatz (Seitenarm des Auslaufs). Fische jetzt zwischen 3,9 und 4,4 cm Länge. Sie stehen in kleinen Schwärmen von 3 bis 5 Stück in verschiedenen der oben erwähnten Kolken. Gegenüber den Verhältnissen am 12.6. eine starke Zunahme des Algenbewuchses (*Spirogyra* cf.

Tab. 4.

Bodenfauna	Drift	Darminhalt
Hydropsyche	*Bosmina*	div. *Cladocera*
Orthocladiinae	div. *Cladocera*	*Chironomidae*
Baetis	*Chlorophyceae*	div. *Algae*
Heptagenia	*Conjugatae*	*Baetis*
Plecoptera	*Diatomeae*	Luftnahrung
Chironomiden	Nauplien	Nauplien

suecia, Coleochaete divergens var. *minor*), der die Steine überzieht. In den Algenwatten Chironomiden und Baetiden, am Boden und an algenfreien Stellen *Hydropsyche* und *Orthocladiinae*. Die Fische zeigen ähnliches Verhalten wie am 12.6., d.h. sie stehen in der freien Strömung und stossen zur Nahrungsaufnahme ruckartig gegen den Strom vor. Die Analyse ergibt folgende Verhältnisse (Tab. 4).

Beide Tabellen zeigen, dass die jungen Salmoniden fast garnicht von der lokal gebotenen benthischen Nahrung leben, sondern dass sie sich am 12.6. vollkommen und am 18.7. zu einem wesentlichen Teil von der allochthonen Nahrung erhalten. Dabei liegt es nahe anzunehmen, dass die scheinbare Ausnützung der Bodennahrung (*Baetis, Chironomidae*) de facto eine Ausnützung der Flussdrift ist. Wie wir schon an anderer Stelle zeigen konnten (MÜLLER 1954), ist dies ein Charakteristikum von *Salmo trutta*. Es erklärt sich dadurch die bevorzugte Eiablage der Salmoniden in solchen Bereichen, denn hier ist den Jungfischen, die zunächst nach dem Schlüpfen in starker Individuenzahl vorkommen, ein nahezu unbegrenztes Nahrungsreservoir gegeben. Ich halte es für eine unabwendbare Voraussetzung für die Entwicklung dieses Fisches, dass er in seinem jüngsten Stadium aktiver Ernährung den Zugang zu relativ kleinen Nahrungspartikeln besitzt, die im freien Wasser des Flusses nur in einer Seedrift auftreten.

4. Die Folgen der künstlichen Veränderung der Seeausflüsse

Es zeigte sich im vorigen Kapitel, dass für die hier behandelten Flussgebiete die Seen auf dem Umweg über die erhöhte Bodentierproduktion von entscheidender Bedeutung für das Wachstum und die Fortpflanzung der Salmoniden in den Stromschnellen sind. Ein Eingriff in dieses System der Wechselbeziehungen zwischen See und Fluss (Seendrift) einerseits und Fluss und See (Erhaltung des Salmonidenbestandes) andererseits, muss zu schwerwiegenden Folgen für den Fischbestand führen.

Zum Studium einer gestörten Beziehung zwischen See und Fluss bietet sich der Stora Lule Älv und sein Abfluss an. An den Seeausfluss dieses grossen Gewässers von 220 km² schliesst sich ein System von Kraftwerkanlagen, die

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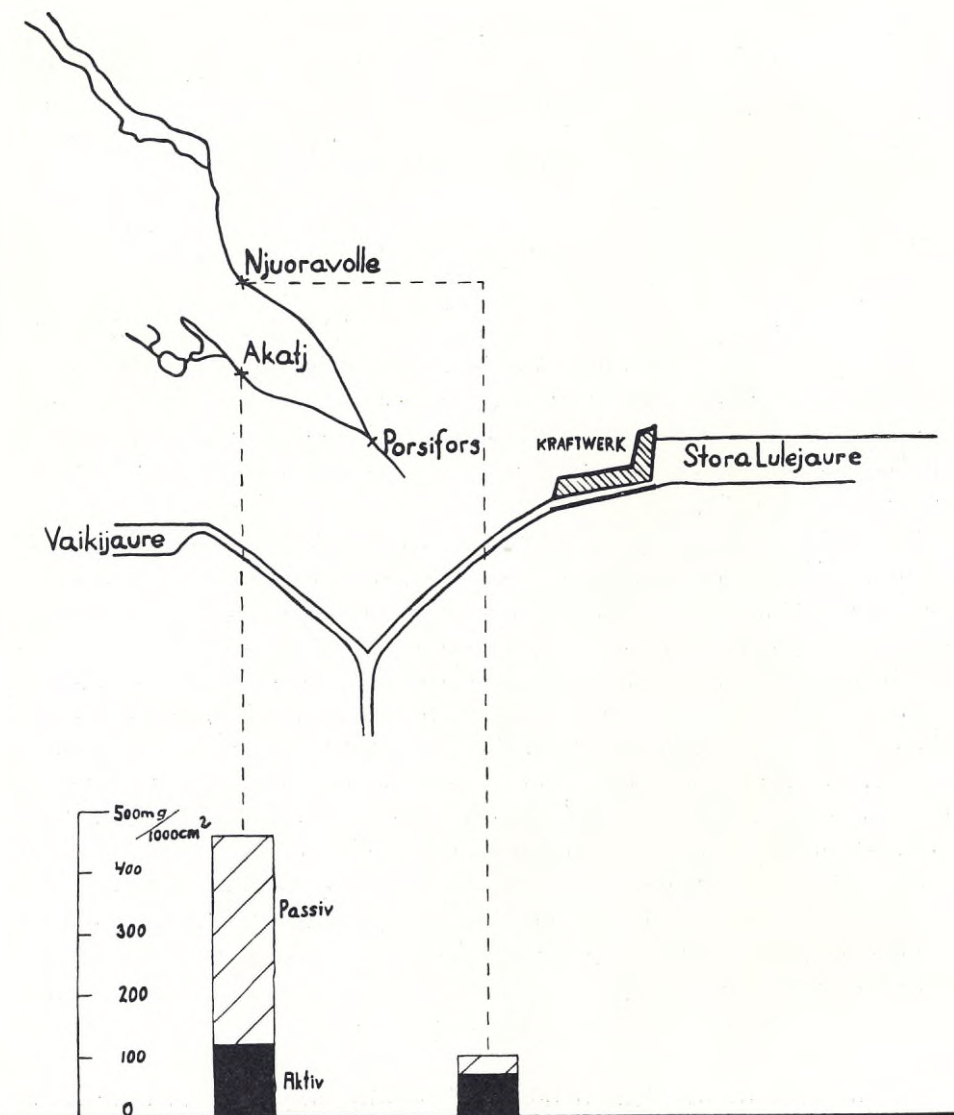
Abb.: 5. Die Verteilung »aktiver und passiver Ernährer« in einem natürlichen und einem
regulierten Flusssystem.

Fig. 5. The distribution of »active and passive feeders« in a natural and a regulated
river system.

das Wasser zum Betrieb der Turbinen aus grosser Tiefe am Staudamm ent-
nehmen und nach unterirdischer Weiterleitung erst in $1/2$ bis 3 km Abstand
dem Flussbett wieder zuführen.

Unsere auf einem reichen Material basierende Untersuchung des Jahres
1954 zeigt für das 24 km lange Stromschnellengebiet zwischen dem Kraft-

werk Ligga und Messaure, dass die typische Ausflussbiozönose, die hier erwartet werden müsste, nicht vorhanden ist. Obwohl ein weit ausgedehntes Seengebiet vorgelagert ist, fehlt ein Einfluss dieses Sees auf die Flussfauna. (s. Abb. 5). Wir sind der Ansicht, dass die Entnahme des kalten, nahrungsarmen Bodenwassers aus dem See (anstelle des in natürlichen Seeausflüssen vorhandenen Auslaufes der warmen, produktionsreichen Epilimnion-Schicht) die Ursache für eine wesentlich herabgesetzte Seendrift ist. Damit sind den passiven Ernährern die Lebensgrundlagen entzogen und es kommt nicht zur Ausbildung der zu erwartenden Ausflussbiozönose. Qualitativ ist der Tierbestand wesentlich verschieden gegenüber allen anderen Stromschnellenbereichen, die oben behandelt wurden, und quantitativ liegt der Wert für die Bodenfauna (Passive : 38,2 — Aktive 66,6 mg/qm/lo) unter dem der natürlichen Vergleichsstrecken. Die aufgefundenen Werte sind die niedrigsten, die von uns im gesamten Flussgebiet des Lule Älvs festgestellt werden konnten. Ausserdem ist das Verhältnis Passive : Aktive hier umgekehrt als in allen anderen Fällen.

Es ist selbstverständlich, dass einer (infolge verringerter oder ganz fehlender organischen Seendrift und der damit verbundenen geringen Menge an Bodenfauna) minimalen Nahrungsgrundlage für die Fische eine sehr herabgesetzte Produktion an Fischen entspricht. Ergänzende Untersuchungen an Fischen dieses Bereiches werden die Aufgabe haben, auch diese Tatsache zu belegen.

5. Regional vergleichende Untersuchungen über die Bedeutung der Seendrift

Untersuchungen, die wir in verschiedenen Bereichen Schwedens anstellten, zeigen, dass es sich bei den geschilderten Wechselbeziehungen zwischen See und Fluss nicht um ein lokales Problem handelt, sondern dass dieser eutrophierende Einfluss der durchflossenen Seen im ganzen Gebiete aufzufinden ist.

Es werden (s. Tab. 5) nach aktiven und passiven Ernährend aufgegliedert für jedes der untersuchten Flussysteme die Besiedlungswerte angegeben, die sich unterhalb von Seen in Stromschnellenbereichen auffinden liessen.

Diese Beobachtungen aus Schweden lassen sich ergänzen durch die Untersuchungen von K. BERG (1948) in der Susaa/Dänemark. Die Tafel 1 der Susaa-Bearbeitung von P. JONASSON dargestellte Besiedlung des Tuel Aa unterhalb des Tuelsö bei Frederikshaab ist in vielen Gliedern (Trichopteren, *Simulium*) eine typische Ausflussbiozönose (l.c. Anhang I p. 208).

Für kleinere Flussysteme (Bäche) Nordschwedens ergeben sich — wie ILLIES 1955 b nachwies — die gleichen eutrophierenden Einflüsse durchflossener Seen auf die Benthos-Besiedlung, wie sie in der vorliegenden Untersuchung für grössere Ströme nachzuweisen waren.

Tab. 5: *Der quantitative Anteil passiver und aktiver Ernährer in verschiedenen nord- und mittelschwedischen Stromschnellen.*

Ort	Passiv (mg/qm/lo)	Aktiv (mg/qm/lo)
Kalix Älv unterh. Kalasjärvi	2.080,0	38,7
Ärs Älv unterh. Åresjö	477,6	88,8
Tandsjö-Ån unterh. Tandsjö	616,4	43,1
Ogströmmen unterh. Ogsjö	371,5	73,7
Värån unterh. Värsjö	386,3	61,8

Weiter südlich auf dem Kontinent zeigte Knöpp in der eingangs zitierten Abhandlung die gleiche Entwicklung.

Wir müssen daher unter Berücksichtigung aller bisher aufgefundenen Parallelen, die trotz ihrer lokalen physiographischen Verschiedenheiten die gleiche Tendenz zeigen, dem Phänomen der Eutrophierung von Fliessgewässern durch dazwischen geschaltete Seen eine über Nordschweden hinausgehende Allgemeingültigkeit zuschreiben.

6. Grundzüge eines Produktionskreislaufes fliessender Gewässer

Unterliegt ein See in seinen Produktionszyklen einer weitgehenden Statik so ist der strömende aquatische Lebensbereich ausserordentlich starken Fluktuationen unterworfen, die auf äusseren Einflüssen beruhen (s. auch Thienemann 1953, Illies 1955 a). Können wir den See in seiner Produktion weitgehend als autark bezeichnen, so zeigt das natürliche Fliessgewässer in den hier dargestellten Beispielen skandinavischer Flüsse eine gegenteilige Tendenz. Unsere Resultate zeigen, dass unterhalb von Seen in der Regel die Organismengruppen der passiven Ernährer beiweitem die der aktiven Ernährer überwiegen. Wir konnten weiter zeigen, dass *Salmo trutta* als Jungfisch aktiv den vom See einströmenden Nahrungszuschuss ausnützt.

Abschliessend sei der Produktionsverlauf in einem skandinavischen Fliessgewässer skizziert, wie er sich nach unseren Beobachtungen ergibt. Betrachten wir dabei eine Stromschnelle zwischen zwei Seen!

Die P r o d u k t i o n s s t u f e umfasst hier die durch Assimilationsprozesse (Algen) gewonnene organische Substanz, die ihrerseits verschiedenen benthischen Organismen (*Ephemeroptera, Plecoptera,* div. *Trichoptera,* div. *Chironomidae, Gastropoda,* div. *Coleoptera*) als Nahrung dient. Diese autochthone Produktion tritt jedoch, wie wir oben zeigen konnten, deutlich zurück gegenüber einer allochthonen Produktion, unter der wir alle von aussen kommenden (Seedrift, Luftnahrung) Einflüsse verstehen wollen. Der Fisch stellt als Konsument letzten Grades den wirtschaftlichen Ertrag dieses Gewässers dar.

Gegenüber dem See, der aufgrund seiner jährlichen Produktionszyklen von diesen abhängige organische Sedimente aufweist, in denen die Reduktions-

prozesse ablaufen, fehlt diese R e d u k t i o n s s t u f e in einem natürlichen Fliessgewässer weitgehend. Reduktionsprozesse laufen zwar ab, abbaufähige organische Substanzen werden aber sehr schnell weggespült, sodass ihre eutrophierende Wirkung gering und prinzipiell verschieden von der eines stehenden Gewässers ist. Ich bin daher der Ansicht, dass die Reduktionsprozesse von denen eine spürbare eutrophierende Wirkung ausgeht, nicht in den Stromschnellen eines natürlichen Flusses ablaufen, sondern dass die hier gebildete und absterbende organische Substanz in Stillwasserzonen oder Seen weitertransportiert und abgelagert wird. Hier erfolgt die Reduktion, deren eutrophieremder Einfluss sich stromabwärts einer anderen Stromschnelle als organische Seendrift mitteilt.

In diesem Sinne müsste in einem Flussystem mit eingeschalteten Stillwasserzonen eine ständige Wechselwirkung Fluss: See und See: Fluss vorliegen, wobei die höchstgelegenen Gewässer aufgrund der noch geringen Intensität der Wechselbeziehungen eine geringere Produktion aufweisen sollten. Mit steigender Intensität des gegenseitigen Austausches müsste ein gesteigerter Ertrag die praktische Folge sein.

Wenn wir zu verschiedenen Einzelgliedern des geschilderten Beziehungsgefüges eindeutige Belege noch schuldig bleiben, so konnten wir auf die Beziehungen See: Fluss doch mit eindeutigem Zahlenmaterial hinweisen und weiterhin zeigen, dass künstliche Eingriffe in das komplizierte Wechselspiel zu einer entscheidenden Veränderung der Lebensabläufe im Fliessgewässer führt.

Summary

The present work deals with the influence of lakes on a river. It is characteristic for Scandinavian streams — here demonstrated on the River Luleälv as an example — that a river is running through several lakes in its course. In this way, an interchange of influence arises, the river having effect upon the lake and vice versa. The lakes do not appear at the lower part of the streams, where they are replaced by broad, slow flowing still water zones (Swedish »sel«) up to 60 kilometres long (see fig. 2). Our investigation was mainly concentrated on the qualitative and quantitative composition of the bentic fauna in the rapids below the lakes. It proved to be a characteristic trait in these rapids that the amount and number of »passive forms of feeders« are by far the most predominant part. Here, the net-marking species of *Trichoptera* (*Hydropsyche, Neureclipsis, Plectrocnemia*), *Simulium* and *Orthocladinae*-larvae are prevailing. Investigations on the nutrition of these larvae showed that they are almost exclusively restricted to feeding on the Phyto- and Zooplankton, which are drifting out of the lake into the river. On this account, the amount of the larvae always depends on the production of plankton in the lake lying above the rapids (see fig. 4). Naturally, the

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amount of »passive» forms decreases with increasing distance to the lake. Under the same conditions, however, the different forms of »active feeders» (*Ephemeroptera, Plecoptera,* various *Trichoptera,* various *Chironomidae*) proved to be very constant as to the amount in which they appeared. The population of bentic animals in the river systems lacking lakes is almost completely derived from »the active feeders» and, therefore, the abundance is mostly very small. In figure 3 a comparison is made between two rivers in Middle Sweden. Both of them present almost equal quantities of »active» forms, but the River Tandsjöån located below a lake has, in addition, an extensive population of passive feeding species of larvae.

Various observations show that young fish (*Salmo trutta*) as well make alimentary use of the plankton drifting out of the lake into the river.

The following conclusions can be derived from the present investigation concerning rapids located below regulated lakes and rivers.

The typical biocenoses of the outflows of the lakes, established in various Swedish river systems, do not appear below regulated parts of lakes and rivers. The amount of »active feeders» always predominates over the passive. The »Capacité biogénique» (in the sense given by HUET) is in this way through an act of interference (building of power plants) always very insignificant. The reason for this is to be found in the fact, that cold, alimentarily poor water is led from the depth of the power dam into the river (see fig. 5). The occurence of »passive feeders» is hereby excluded. Investigations are going on as to the amount and composition of the organic drift received by rivers from natural and regulated lakes.

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Studies on the Feeding Habits of Trout and Char in North Swedish Lakes

By Nils-Arvid Nilsson

Contents

1. Material and Methods

The present paper is based on an investigation of about 2,400 trout (*Salmo trutta* L.) and char (*Salmo alpinus* L.) from three lakes in the North-Swedish mountain region (cf. map, fig. 1). Of these, analyzis of the stomach contents was made of 659 trout and 995 char. During the years 1944—1949 the fish were caught by members of the staff of the Institute of Freshwater Research and in 1954 mostly by professional fishermen. The fishing tackle used as a rule consisted of gill-nets; in the winter the fish were caught by »bobbing» from the ice. The various fishing stations were chosen so as to represent as many aspects of the fauna of the lake as possible.

Every fish was carefully weighed and measured at the fishing station and the stomachs were preserved in 4 % formaline. In the laboratory the content of every stomach was examined under a microscope, and every food item was measured volumetrically. To get a numerical expression of the significance of the various food objects three methods were used:

1. The percentage of every food item was calculated for every stomach. The figures obtained were summed and divided by the number of stomachs investigated. This method expresses the average dietary state of the population during a certain time or at a certain place and is marked »volumetric», (V), in the tables.

2. The presence of the different food objects was noted and calculated as a percentage of the stomachs investigated. This method is marked »frequency», (F), in the tables.

3. The predominant food objects were noted and calculated as percentage of the stomachs investigated. This method is marked »dominance», (D), in the tables.

The figures of method 1 have been used when constructing the different diagrams illustrating the text as they are the most accurate. The numbers, as a rule, were calculated per month. Calculations were made on small samples consisting of 10 or less fish, but none of the diagrams are based on samples of less than 20 specimen per month.

The identification of the food animals was taken to a sufficient level for the purposes of discussion of the problems of significance in this paper. Thus the crustaceans were identified to species, the mollusca to genera, the neuroptera to orders, the chironomidae to genera and the terrestrial insects to families.

In connection with the netting of fish in Lake Blåsjön, an investigation of the bottom fauna and of the crustacean plankton was carried out. Quantitative bottom-samples, taken with an EKMAN-BIRGE sampler, have partially been treated by BRUNDIN (1949) and A. MÄÄR (unpublished), and qualitative plankton-samples, taken with a plankton-net, by H. LÖFFLER (1953).

To study differences in distribution between trout and char within the same lake a special test-fishing was carried out in Lake Ransaren. This was done in the following way: gill-nets with different mesh-sizes were mixed and linked together in long chains containing 6—9 nets. These were placed at three different fishing-stations, each chain with one end near the shore, the other one pointing to the centre of the lake. The length of every net was 27—30 metres, the height 5 feet. As the nets were never fully stretched a chain with 9 nets as a rule reached about 250 metres. When fishing the nets every fish taken was carefully noted as to species, size, depth of the catch and distance from the shore. The percentage distribution of each fish species over one season was calculated per net length. (cf. diagrams, p. 189).

A preliminary report based on part of the present material was earlier published in German (NILSSON 1955).

2. The Lakes

Lake Blåsjön is situated in the upper part of the pineforest region in the province of Jämtland, about 64° 50′ north latitude and 434 metres above sea level. The bedrock consists of so called »seve»-chist, poor in lime. The area of the lake is 41.4 km² and its greatest depth 152 m. It is strongly oligotrophic and oligohumous. From L. BRUNEAU (in manuscript), LÖFFLER (1953) and
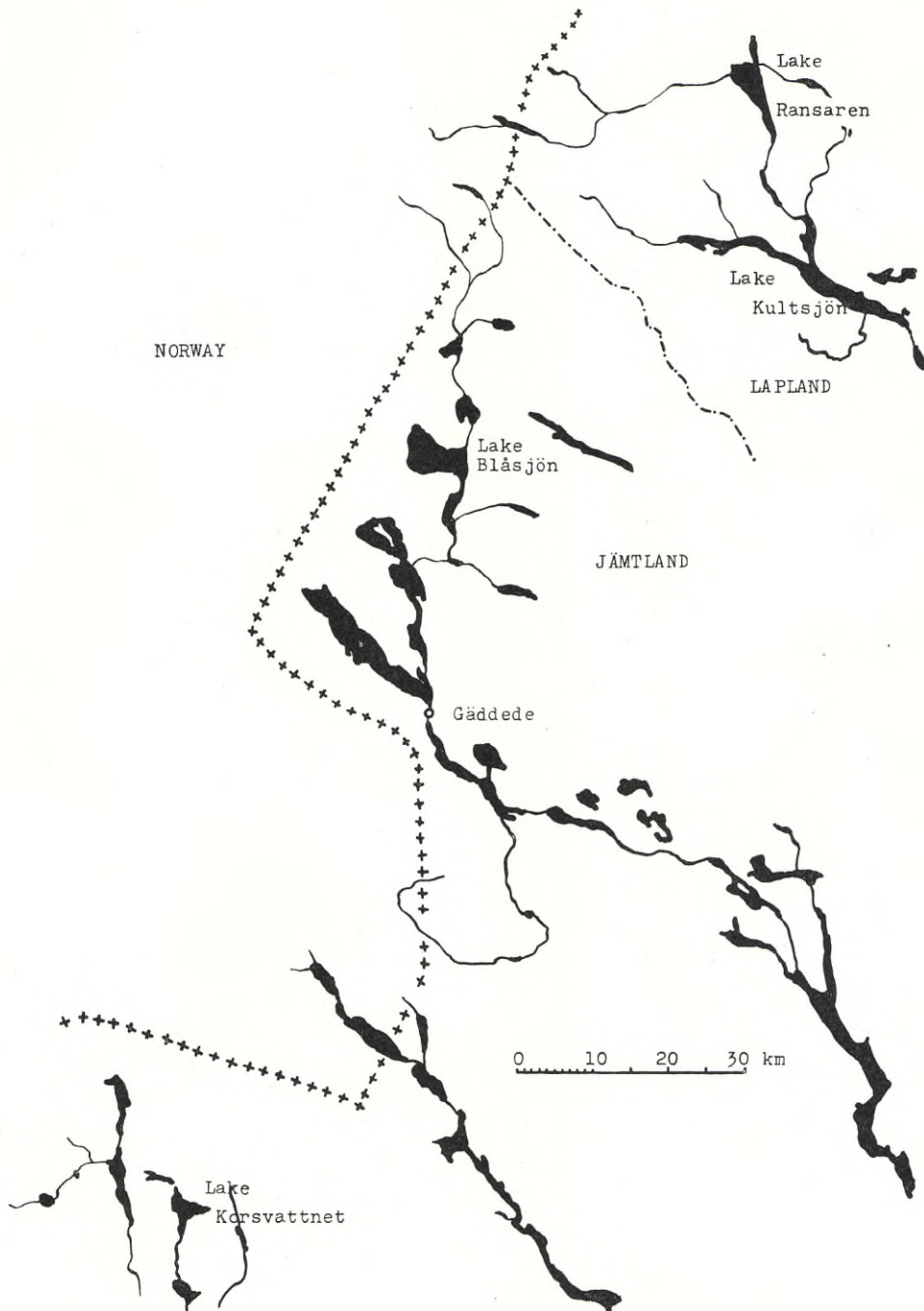
Fig. 1. The geographical situation of Lakes Ransaren, Blåsjön and Korsvattnet.

Table 1. Milieu factors in Lake Blåsjön. The samples are taken at
the water surface.

		Date	Author
Transparency, m	9—13	Summer 1944—1949	MÄÄR
Conductivity, $\varkappa_{18} \cdot 10^6$	24.8	31/10 1952	LÖFFLER
Alkalinity, mekv/l	0.15	7/2 1950	BRUNEAU
pH	6.7—7	Summer 1944—1949	BRUNEAU, MÄÄR
Ca, mg/l	3—4	» » »	BRUNEAU
P, mg/l	12	31/10 1952	LÖFFLER

MÄÄR (in manuscript) the following data representing different milieu factors have been extracted (Table 1).

Stable temperature stratification in the lake does not take place before the beginning of July. During warm summers the temperature of the surface water can rise to more than 20° C. The following data for 1946 and 1949 may be used as examples of the variations in water temperature in Lake Blåsjön (Table 2).

The ice breaks up at the beginning or middle of June and the water is frozen over again in December.

The non-planktonic plants of the lake are exclusively submersed, consisting of dispersed spots of *Isoëtes, Nitella,* watermosses, etc. (BRUNDIN 1949).

Unfortunately the results obtained by MÄÄR from his examinations of his collections of bottom animals are not yet published. Here only a collation of MÄÄR's calculations of the bathymetrical distribution of the different organisms in the lake are given. The diagram, fig. 2, and table 10 are based on a series of 158 bottom samples taken by MÄÄR with an EKMAN-BIRGE bottom-sampler at different depths and different parts of the lake during the years 1945—1948. Though the figures representing the number of individuals give a somewhat false picture of the relative quantity of the different animal groups in the bottom fauna, the predominance of the four groups of *Nematodes, Oligo-*

Table 2. Water temperature in Lake Blåsjön during 1946 and 1949
(From MÄÄR; in manuscript).

	1946			1949	
Date	Depth, m	Temperature, °C	Date	Depth, m	Temperature, °C
2/7	0	4.3	14/7	0	9.3
	15	4.5		10	6.2
20/7	0	20.3	4/8	0	11.2
	3	12.4		10	10.3
	5	11.2		15	8.0
	10	9.2		20	7.1
	20	6.5	25/8	0	10.7
7/8	0	13.9		10	9.7
	10	12.0		20	9.1
	15	9.0			
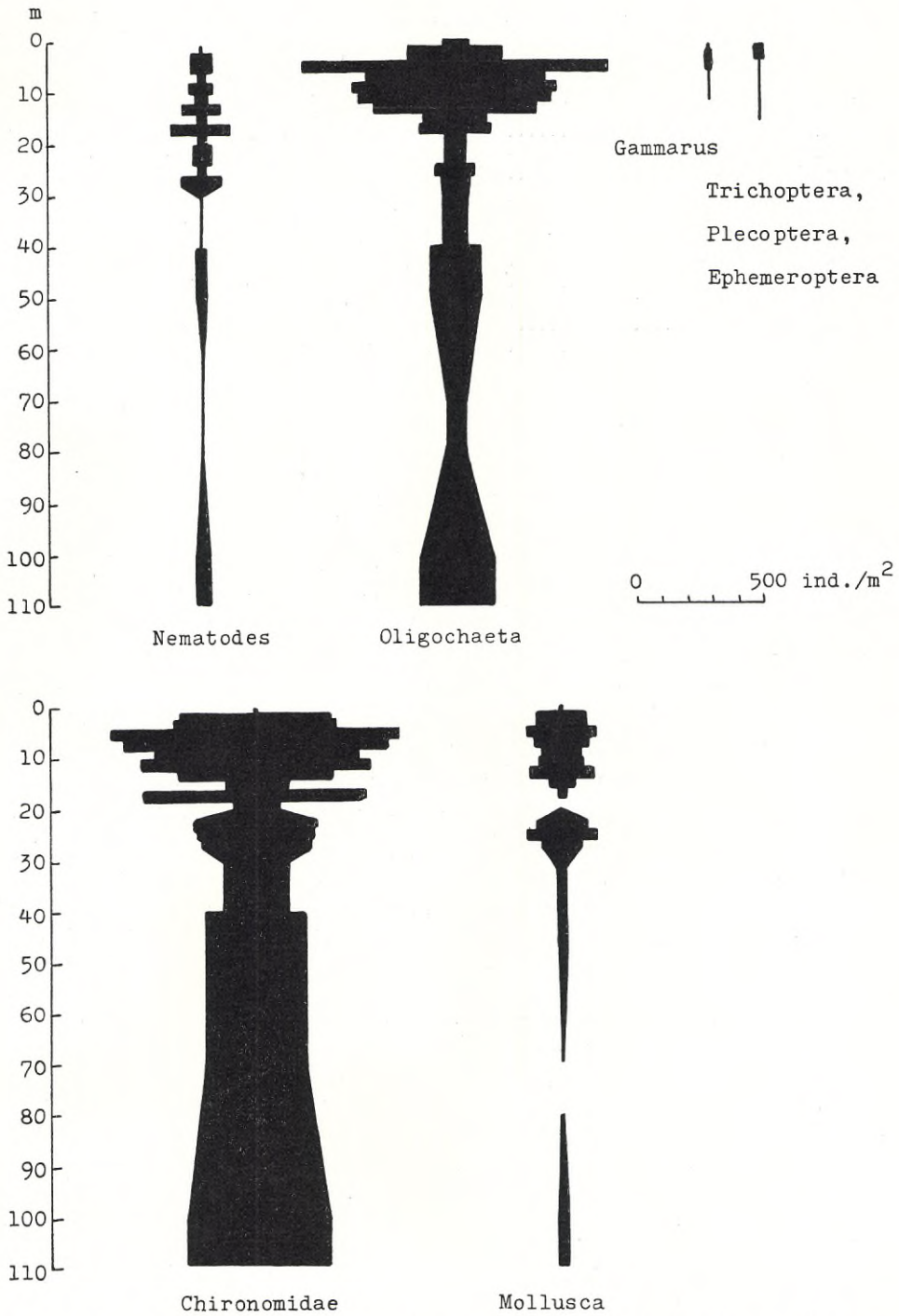
Fig. 2. Bathymetrical distribution of some bottom animals in Lake Blåsjön. Based on unpublished material by MÄÄR. Ordinate: depth in m, abscissa: individuals/m².

Table 3. Seasonal occurrence of the different species of planktonic crusta-
ceans in Lake Blåsjön.

		Maximum
Eurycercus lamellatus	July—October	August
Sida crystallina	July—August	—
Holopedium gibberum	June—October	September
Daphnia longispina	April—October	August
Bosmina coregoni	June—November	August
Polyphemus pediculus	July—August	August
Bythotrephes longimanus	June—October	July—August
Heterocope saliens	July—October	August
Diaptomus laciniatus	July—August	—
Diaptomus laticeps	August—October	—
Cyclops scutifer	April—November	July, September

chaeta, Chironomidae-larvae and *Mollusca* is most obvious. For most of the
animals the maximal abundance is found in the upper littoral region at the
depths of 4—10 m. The highest figure for density of population of all the
bottom fauna, 2,853 ind./m², was found at the depth of 4—6 m.

The *Chironomidae* were carefully investigated by BRUNDIN (1949). The
most abundant species both in the littoral and profundal regions is *Hetero-
trissocladius subpilosus* (KIEFF.) EDW. The important part played by this
and other *Heterotrissocladius*-species in the bottom fauna of Lake Blåsjön
and other Scandinavian subarctic lakes has caused BRUNDIN to propose the
term »*Heterotrissocladius*-lakes».

If comparing the bottom faunas of Lake Blåsjön and the South Swedish
oligotrophic lakes investigated by BRUNDIN (1949) three facts may be noted:

1. The relative abundance of the different bottom animals is on the whole
the same, the predominant animals being *Nematodes, Oligochaeta, Chirono-
midae*-larvae and *Mollusca*.

2. As a consequense of the general trophic standard of the lake the num-
bers of individuals per m² are lower in Lake Blåsjön than in the South Swed-
ish lakes, the average densities in the littoral of the South Swedish lakes
Innaren, Stråken and Skärshultsjön varying between 5,000 and 26,000
ind./m² in Lake Blåsjön between 130 and 2,850 ind./m².

3. The maximal abundance is found at a greater depth in Lake Blåsjön
than in the South Swedish lakes, possibly due to the lack of shallow bays
with emersed vegetation.

LÖFFLER found 13 species of planktonic crustaceans in Lake Blåsjön,
10 of which were in significant quantities. An extract of LÖFFLER's tables
combined with experiences from the present investigation gives the following
picture of the occurrence of planktonic crustaceans in Lake Blåsjön (Table 3).

It is clear from the table that all the planktonic crustaceans have their
maximal abundance in summer and autumn, a fact that has been established
before from Scandinavian mountain lakes (cf. EKMAN 1904, DAHL 1930, LIND-
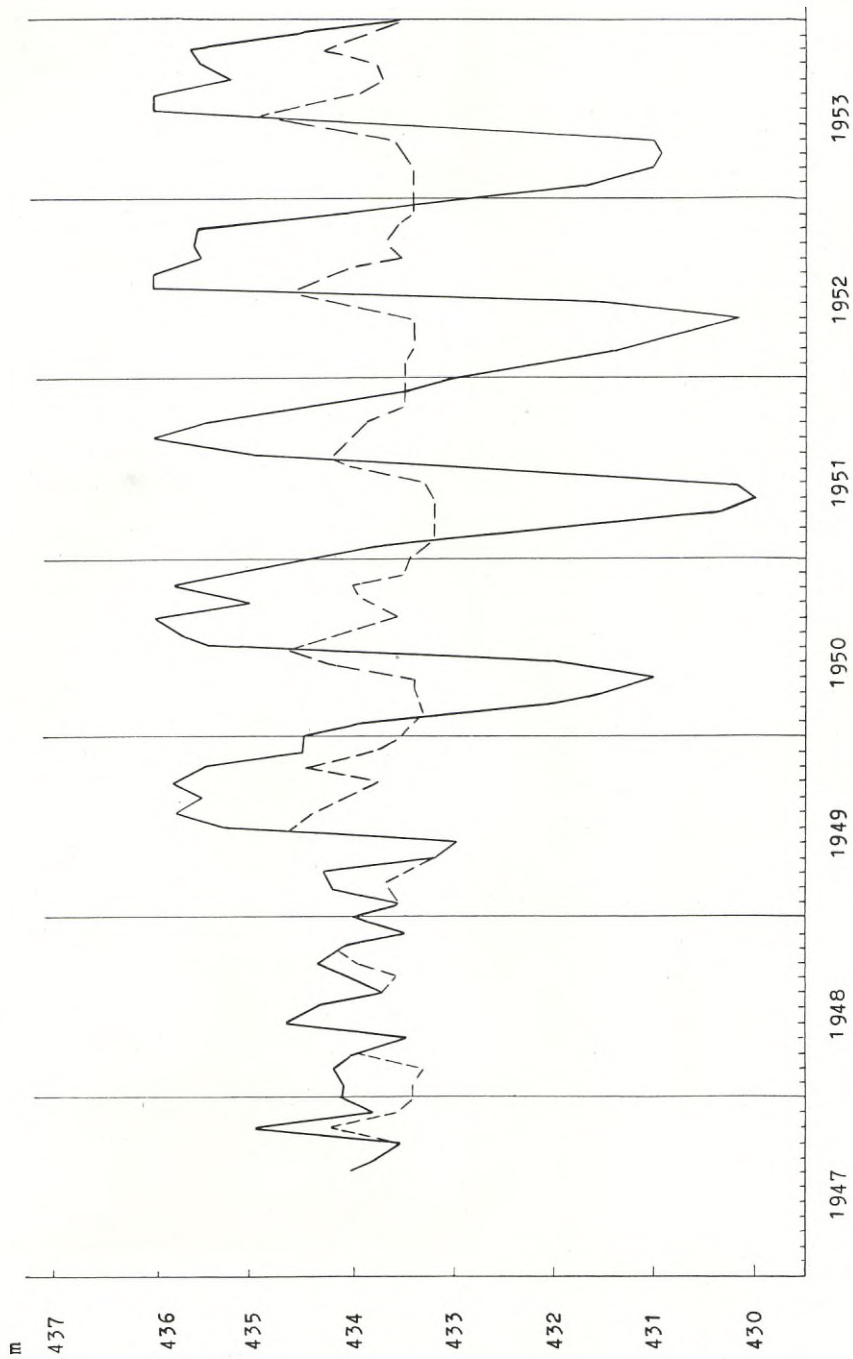
Fig. 3. The water level fluctuations in Lake Blåsjön. —— =regulated water level, — — =unregulated water level.

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STRÖM 1952) and is of fundamental significance when discussing the feeding habits of char.

The lake was dammed up in 1947. For storage purposes a dam was built at the outflow of the River Blåsjöälven, which makes it possible to raise the surface of the lake from normal waterlevel (434) to 436 m above sea level or to lower it to 430 m above sea level. The damming up as a rule occurs in the summer and autumn (June—January) the lowering in the winter (February—May), which means that large areas of the bottom are drained in the winter, while large new areas are inundated in the summer. The fluctuations of water level in Lake Blåsjön are shown at the diagram, fig. 3.

Lake Ransaren is situated in the upper part of the pineforest region of southern Lapland, about 65° 15′ north latitude and 583 m above sea level. The area of the lake is 21.2 km² and its greatest depth 60 m. Its general physical conditions very much resemble those of Lake Blåsjön. Besides trout and char the lake contains burbot (*Lota lota* L.) and minnow (*Phoxinus phoxinus* L.).

Lake Korsvattnet is situated in the lower alpine belt of the district of Jämtland, about 63° 52′ north latitude and 741 m above sea level. Its area is 10.8 km² and its greatest depth 90 m. It is strongly oligotrophic and oligohumous. Its vegetational period extends from June to December. The only fish species in the lake is char.

3. Feeding Habits of Trout and Char in Lake Blåsjön

Seasonal variations

It is evident from several earlier investigations (EKMAN 1912, HUITFELDT-KAAS 1935, LINDSTRÖM 1947, 1955, ALLEN 1951, MÜLLER 1954), that there exist a seasonal variation in the feeding habits of trout and char. The present investigation strongly confirms the fact.

To facilitate the interpretation of the diagrams the various food items have been brought together into three main groups: »*Entomostraca*» (in the tables corresponding to *Copepoda-Eurycercus*), »bottom food» (*Gammarus-Coleoptera* i.) and »hatching and flying insects» (*Trichoptera* p.i.-terr. *insecta*), the variations of which in the food of the fish are clear from the tables, fig.:s 4—6. Four tendencies, obvious in the diagrams, may at once be pointed out:

1. The feeding habits of both trout and char are varying not only seasonally but also from year to year.

2. Bottom food during the ice-free season is of much greater importance in the food of trout than it is in the food of char.

3. *Entomostraca,* (mostly planktonic), during the ice-free season is of great importance as food of char, but of very little importance to trout.

4. Hatching and flying insects are to a great extent consumed both by trout and char.
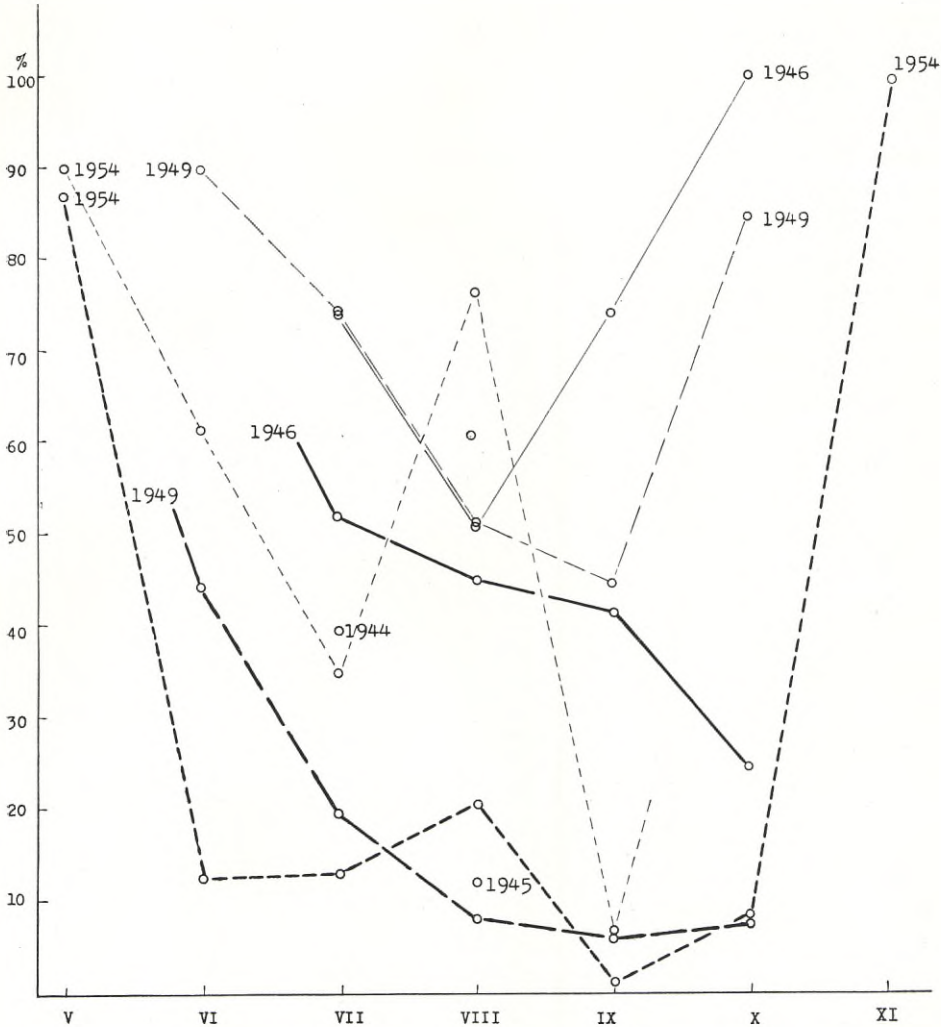
Fig. 4. The consumption of bottom food by trout (thin lines) and char (coarse lines) in Lake Blåsjön. ———=1946, — —=1949, – – –=1954.

Though there are great variations from year to year, a certain seasonal rythm which is repeated every year, can be discerned. In trout this can be characterized as a change between bottom food and hatching and flying insects. The bottom food above all consists of *Trichoptera*-larvae with a considerable addition of *Chironomidae*-larvae (in winter[1]), *Gammarus*, *Mollusca*, *Ephemeroptera*-larvae, *Plecoptera*-larvae and *Tipulidae*-larvae (in summer). Of the insects the most important part is played by those of terrestrial origin,

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[1] When used in this paper »winter» means the iced season (December—middle of June).
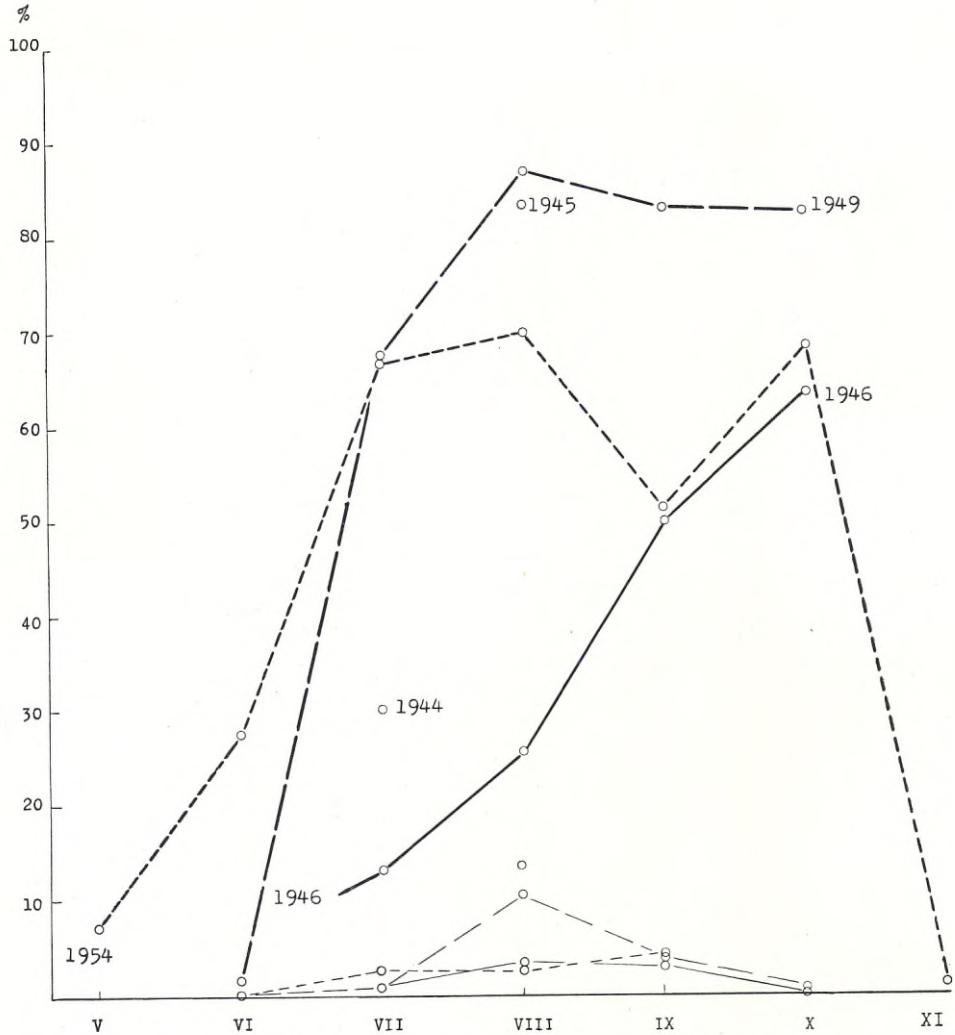
Fig. 5. The consumption of *Entomostraca* by trout (thin lines) and char (coarse lines) in Lake Blåsjön. ——=1946, — —=1949, - - - -=1954.

falling on the surface of the lake. During their hatching time pupae and imagines of *Trichoptera* and *Chironomidae* are consumed to a considerable extent.

The diet of char changes between bottom food (above all consisting of *Gammarus*, *Plecoptera*-larvae and *Chironomidae*-larvae) in winter, hatching and flying insects (above all *Chironomidae*-pupae) in summer and *Entomostraca* in summer and autumn.

When searching for the causes of these variations it is necessary to study the possible seasonal variations in abundance of the lake's fauna. From the
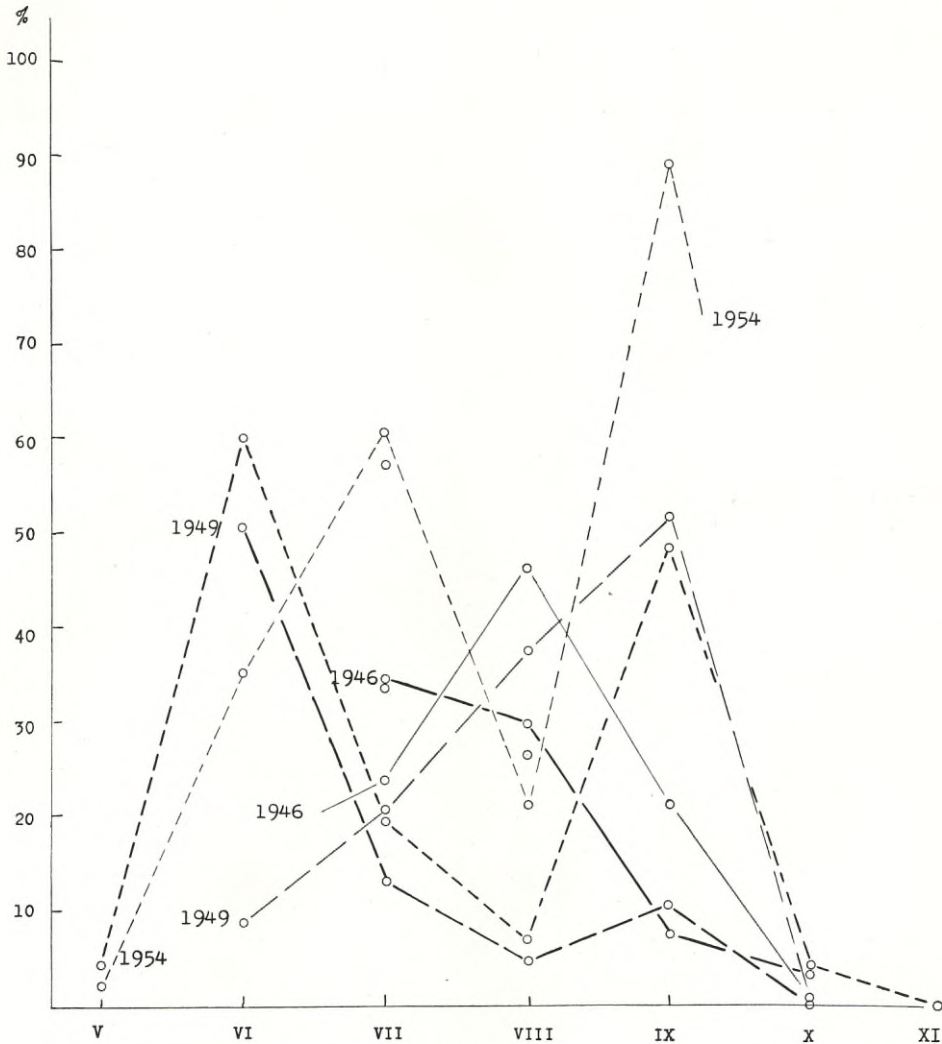
Fig. 6. The consumption of hatching and flying insects by trout (fine lines) and char (coarse lines in Lake Blåsjön. ——=1946, — —=1949, ---=1954.

bottom investigations of Lake Blåsjön we get no information in that respect so we have to turn to other works. It is in fact evident from several investigations of the bottom faunas of Scandinavian lakes (Yxtasjön, ALM 1922, Høvrebutjern and Birisjøen, OLSTAD 1925, DAHL 1930, Innaren, BRUNDIN 1949) that there are regular variations of this sort. Also JUDAY (1922) in United States and LUNDBECK (1926) in Germany have demonstrated seasonal variations in the abundance of the bottom fauna. If taking into account some of the important fish food organisms of bottom origin we obtain the following collation of the investigations mentioned:
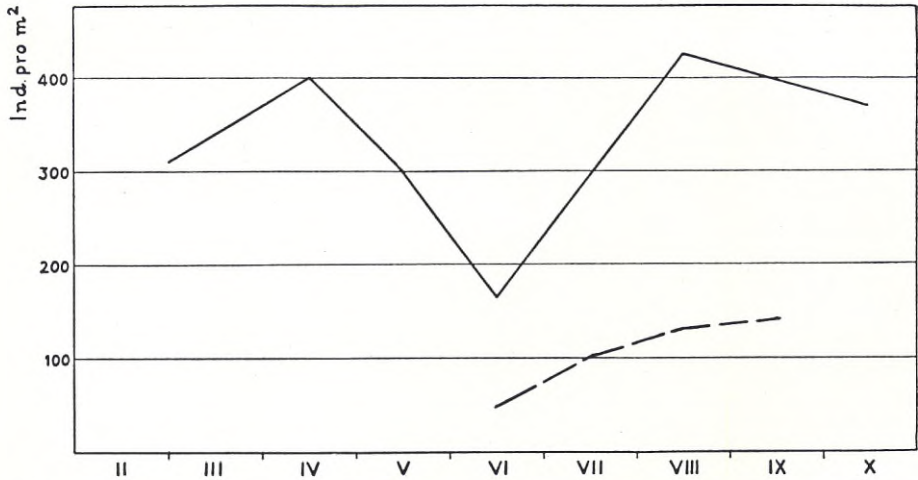
Fig. 7. Seasonal changes in the abundance of *Pisidium* in Lake Innaren. (———) and Lake Birisjøen (— —) (After BRUNDIN 1949 and OLSTAD 1925).

Mollusca. The most accurate calculations concern *Pisidae*. Fig. 7 is taken from BRUNDIN's work and OLSTADs data from Lake Birisjøen are plotted in the diagram for comparison. Both investigations indicate a minimal abundance in June. Concerning *Gastropoda* there are no convincing data available.

Gammarus. According to DAHL's revision of OLSTAD's data from Lake Birisjøen Gammarus has a minimal abundance in July: June 130, July 102, August 167 and September 176 individuals per m². The basic figures are however too variable to be convincing. I. SØMME (in SCHMIDT-NIELSEN 1939) has stated that *Gammarus* has its maximal abundance in late winter because its reproduction period occurs at that time.

Trichoptera-larvae. As to the seasonal variation BRUNDIN (loc. cit. p. 199) states: »Das Material zeigt, dass die Abundanz einer ausgeprägten Saisonvariation unterworfen ist. Berechnen wir die mittlere Abundanz in der mittleren und unteren Litoralzone während der verschiedenen Jahreszeiten, zeigt es sich, dass die Abundanz im Winter am höchsten ist (260 Ind. pro m²). Während des Frühlings und Sommers sinkt die Abundanz allmählich und beträgt im Mai 160, im Juni 115 und im August nur 38 Ind. pro m². Im Oktober sind die Larven wieder häufig (190 Ind. pro m²).»

Ephemeroptera-larvae. On the larvae of *Ephemera vulgata* in Lake Innaren BRUNDIN (loc. cit. p. 197) states: »Das Schlüpfen der Imagines während des Sommers verursacht starke Jahreszeitliche Verschiebungen in den Abundanzzahlen. So gibt es in 4 bis 10 m tiefe durchschnittlich: während des Winters und Frühlings 40—70, im Juni und August nur 9 bzw. 14 und im Oktober 50 Ind. pro m².»

Plecoptera-larvae. In the North Swedish lakes under investigation the *Ple-*
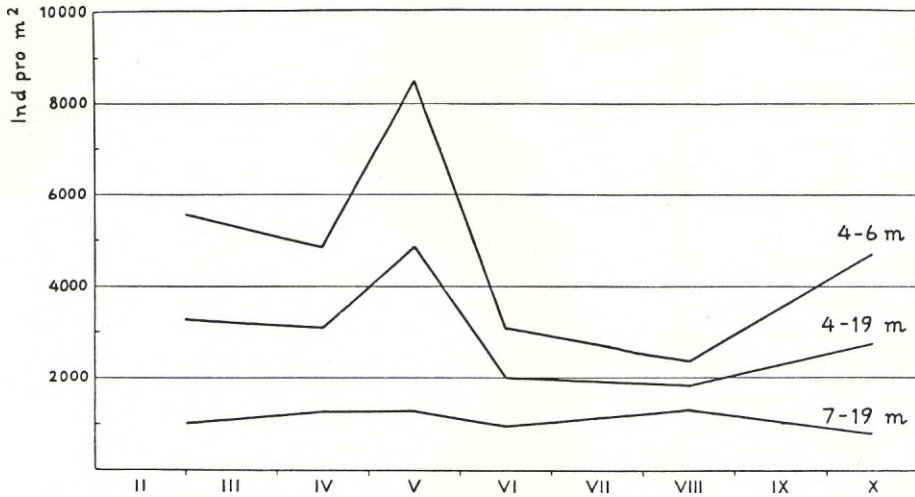
Fig. 8. Seasonal changes in the abundance of *Chironomidae* in Lake Innaren.
(After BRUNDIN 1949).

coptera regularly are the earliest insects to hatch in spring (also in late winter through the angler's »bobbing-holes»), which indicates that the abundance of the *Plecoptera*-larvae decreases very early.

Chironomidae-larvae. Fig. 8, taken from BRUNDIN (1949), shows the heavy decrease in the abundance of *Chironomidae*-larvae during the summer. About the apparent maximum in May BRUNDIN (loc. cit. p. 126) states: »Das Maximum im Mai bedeutet sicher keine Zunahme der tatsächlichen Individuenzahl, vielmehr ist dasselbe darauf zurückzuführen, dass der rasche Zuwachs der Larven im Frühjahr — von der Zunahme der Wassertemperaturen nach dem Eisbruch verursacht — es mit sich bringt, dass die Probenahmen effektiver werden».

Total weight of the bottom animals. ALM (1922, p. 45) has calculated the seasonal variation of the total weight of all the bottom fauna per m² in Lake Yxtasjön over a period of three years. Though there are heavy annual variations in ALM's data, they on the whole seem to indicate a maximal abundance in winter and a corresponding minimal abundance in summer. This also agrees with LUNDBECK's (1926) data from North Germany, though of course the differences in the geographical situation of the lakes result in differences in the seasonal effects. In this connection it may also be emphasized that Lake Blåsjön is situated far north from both the German and the South Swedish lakes, which means that the seasons in e.g. Lake Innaren cannot in detail be compared with the seasons in Lake Blåsjön.

The important fact, however, to be noticed here is that most of the bottom food organisms (above all the larvae of the aquatic insects) decrease in

abundance in summer — the time when there is also a decrease in the share of the bottom organisms in the food of the fish.

As regards the planktonic crustaceans it has been emphasized above (p. 168) that in the lakes investigated there is a marked maximal abundance during the ice-free season, which has a most obvious effect on the feeding habits of char (cf diagram, fig. 5 and LINDSTRÖM 1955).

The two most important food items occuring in the main group of »hatching and flying insects» are the *Chironomidae*-pupae and the terrestrial insects. These naturally occur during the ice-free season. BRUNDIN has calculated the seasonal changes in the number of emerging *Chironomidae*-species in the subarctic lakes of Jämtland (among these Lake Blåsjön); the diagram fig. 9 is taken from BRUNDIN's work. The curve shows an obvious maximum in July—August, which also can be discerned in the feeding-habits of the fish.

It is *a priori* obvious that the supply of terrestrial insects must be dependant upon a lot of more or less random factors: air temperature, force and direction of the wind, life cycles of the insects in question, and so on. Certainly of great importance are the winds that, especially in warm summers, fall over the cold mountain lakes, bringing large quantities of insects, some from great distances (cf PALM 1949). Mass-development of insects, occurring especially in *Lepidoptera* in certain years is another phenomenon bringing great quantities of food to the lake. A sensational example which occurred in 1954 was provided by the *Geometridae Oporinia autumnata,* which developed in great masses in the North-Swedish birch-wood region. During its hatching period in September it was quite predominant in the food of both trout and char, constituting 89 % of the food of trout, 49 % of char, occurring in 94 % of all trout stomachs investigated, 58 % of all char stomachs (cf. tables 11 and 12).

The above facts lead us to suppose that there might be considerable annual variations in the consumption of the main food of »hatching and flying insects», which is also evident from the diagram, fig. 6.

There is a trend very obvious to the student of salmonid stomachs: as a rule each stomach contains one food object with very marked dominance, which gives the impression that it has been chosen very carefully by the fish. That is the cause of the very striking conformity between the numerical results reached by the »volumetrical» and the »dominance»-methods, the deviation very rarely exceeding 5 % (cf. tables 11 and 12). The choice often seems to be very subtle; for example *Heterocope* dominating one stomach, *Holopedium* another, *Heterotrissocladius*-pupae dominating one stomach, *Procladius*-pupae another, and the two food objects rarely are mixed though they occur in the fauna at the same time. This choice tendency, which has
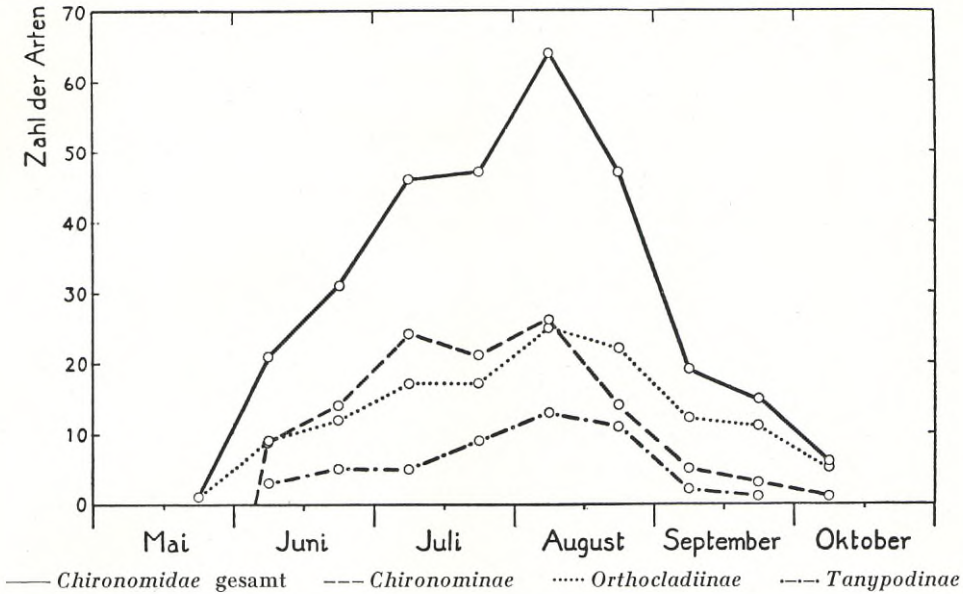
Fig. 9. Seasonal changes in the number of chironomid species emerging in the subarctic lakes of Jämtland. After BRUNDIN (1949).

been long observed by anglers using artificial fly, is not equally obvious during all seasons or in relation to all food objects. It indicates, however, that the feeding habits of the fish are ruled by a complex behaviour mechanism, involving a sort of conditioning on a certain food object being in abundance at a certain time. Very promising experiments, supporting this idea, have been carried out on grayling (*Thymallus*) with artificial flies of different colours. It was shown that the fish respond to sign stimuli of colours, which are at the same time abundant in the fauna of the stream (T. ROOS, verbal communication, cf. also LINDSTRÖM 1955).

To sum up, the seasonal variations in the feeding habits of trout and char seem to depend on seasonal variations in the fauna itself, affecting the two species in different ways, depending on differences in their behaviour mechanism.

The idea that other factors than fluctuations in the abundance of the fauna should also influence upon the seasonal variation in the feeding habits of the fish may, however, not be quite excluded. An inherent preference to different food objects during different seasons as reported in birds (NOLL and TOBLER 1924) would render interesting problems to experimental work. It is also obvious that seasonal movements of the fish (e.g. depending on reproduction or preference to certain water temperatures) may to a certain degree affect their feeding habits.

12

Annual variations. Effects of lake regulations.

It has already been mentioned above that there are considerable annual variations in the feeding habits of the fish, a fact that is also evident from the diagrams, fig:s 4—6. Taking the two food items with least random variation, the »bottom food» and the »*Entomostraca*», the different years under consideration may be characterized as fallows:

1946. »Bottom food» was of extraordinarily great, »*Entomostraca*» of very little importance.

1949. »Bottom food» was of little, »*Entomostraca*» of very great importance. This was most noticeable for char; the same tendency, however, can also be discerned for trout.

1954. »Bottom food» was of very little, »*Entomostraca*» of greater importance.

There are reasons for presuming that these variations in the relative importance of the different food objects depend on any of the following phenomena:

1. High production of one or more food organisms.

2. High production of all food organisms.

3. Low production or otherwise low abundance of one or more food organisms.

4. Low production or otherwise low abundance of all food organisms.

5. Changes in the feeding habits of the fish depending on other phenomena.

Naturally certain of the above possibilities could be combined with each other.

Knowledge of the annual variations in the feeding habits of the fish alone is not enough to make possible an interpretation on the above basis. Unfortunately the investigations of the fauna of the lake do not shed much light on the problem. Two factors profoundly affecting the production of the organisms of the lake will, however, be dealt with here:

1. Temperature, which in most cases may be positively correlated to solar radiation, the source of energy in the primary production. When dealing with fish production the temperature itself may, however, be as well important as it is directly affecting the activity of the fish and also in an important factor affecting the primary productivity of the lake as well as production and transport of terrestrial animals serving as food of the fish.

2. Lake regulations.

As the series of water temperature measurements taken in Lake Blåsjön do not present even series over all years under consideration, air temperatures have been used as the general basis for the following discussion.

The diagram, fig. 10, and table 14 show the mean temperature at Gäddede (cf. map, fig. 1) in April—October during the years under consideration, and the approximate surface water temperature at the 15th of April—July,
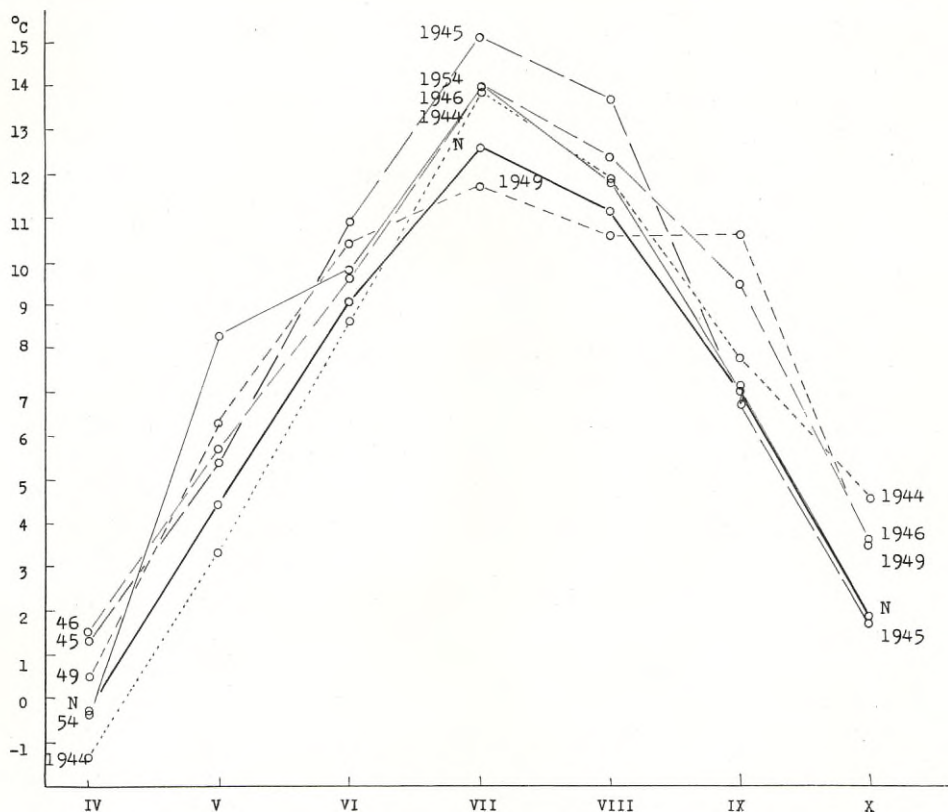
Fig. 10. The mean air temperature at Gäddede in April—October 1944, 1945, 1946, 1949 and 1954, and the normal air temperature (1901—1930), (N).

1946 and 1949 in Lake Blåsjön. On the basis of these temperature measurements the following characteristics can be discerned:

1946: This year was the third in a series of years with very hot summers. The high air temperature heated the epilimnical water to a considerable extent; the maximum surface water temperature, 20,3° C was reached in July (cf. table 2). It can be presumed that there was a very high organic production in the lake this year, a presumption that is well supported by the fact that the quality of the fish this year was very high (cf. next chapter and table 4).

1949: The summer temperature this year was abnormally low, the mean temperatures of July and August both being below normal temperature (1901 —1930). The maximal surface water temperature, 10.7° C was not reached before the end of August. Though the mean summer temperature of the preceding year was relatively high, a relatively low organic production could be presumed for 1949, which is also indicated by the low quality of the fish this year (cf. table 4).

1954: Both spring and summer temperature this year was very high. As also the summer of the preceding year was a hot one, a high organic production could be presumed, which is also indicated by the high quality of the fish (cf. table 4).

At page 170 and the diagram, fig. 3 the fluctuations of water level due to the regulation of Lake Blåsjön have been represented. It may be pointed out that the regulation started in 1947 on a very restricted scale, which only involved small periods of damming up. No draining occurred before 1950, after which year the lake was regulated to the full extent.

Since lake regulation have become common in Scandinavia, several investigations have been made to judge to what degree the damming up and lowering of the water level affect the fish and the fish food organisms (cf. DAHL 1926, 1932, HUITFELDT-KAAS 1935, RUNNSTRÖM 1946, 1951, 1952). On the basis of these investigations some generalizations can be made as to the effects of a regulation of the type occurring in Lake Blåsjön:

1. As an effect of the damming up and the immediate draining some bottom organisms (above all *Pisidae* and *Gammarus*) decrease in abundance or disappear.

2. As an effect of the damming up, which during the first years means that the nutrients of new areas are made available, the bentic *Cladocera* (e.g. *Eurycercus*) and possibly also the crustacean plankton increase in abundance.

3. The fish wander into the overflowed areas feeding on the abundant crustaceans and the drowned terrestrial animals.

4. As an effect of the superabundance of food animals in the overflowed areas, the fish increase in growth, but after some years, decrease again due to overcrowding (RUNNSTRÖM 1951).

Returning now to the annual variations in the feeding habits of the fish some possibilities to an interpretation may be pointed out:

1946: Postulating that there was a high organic production this year, there is no reason to believe that this was valid only for the »bottom food» (in this case mainly *Gammarus*) and above all there is no reason to believe that the curves illustrating the consumption of plankton in 1946 and 1949 (fig. 5) also illustrate the true relation between the *production* of plankton in the lake these years. The extensive consumption of this food thus should not depend on »*Entomostraca*» or »hatching and flying insects» being in deficit, but to a superabundance of food on the whole and a preference of both trout and char for »bottom food».

1949: As there are good reasons to suppose that there was a relatively low organic production this year it seems likely that the supply of »bottom food» was not great enough to feed both trout and char without strong competition. The lake, however, was dammed up this year, which possibly caused a

great production of crustacean plankton (cf. above). As plankton is easily available to char the extensive consumption of »*Entomostraca*» by this species fits in well on the supposed with this presumption. Any important increase in the trout's consumption of bentic *Cladocera,* as reported by DAHL (1926), was not observed.

1954: The lake this year had been fully regulated for 4 years. Though no bottom organism seem to have disappeared because of the regulation, the low consumption of »bottom food» both in trout and char seems to be a likely consequence of a decrease in abundance caused by the regulation (cf. above). For the rest the feeding habits of the fish this year was characterized by the very great supply of terrestrial insects, above all the butterfly *Oporinia autumnata.*

Summing up, the annual variations in the feeding habits of the fish seem to depend on variations in the organic production in the lake or other changes in the supply of food animals. The regulation of Lake Blåsjön is supposed to have caused an increase in the importance of planktonic and bentic *Entomostraca* as food of the fish, and a corresponding decrease in the importance of bottom animals.

Variations in the condition of the fish

Of both theoretical and practical interest is the question of the degree to which the seasonal and annual variations in the food composition may influence the growth and condition of the fish. It has been established in Sweden that hot summers can have the effect of an increased growth on certain species of fish. Thus OLOFSSON (1932) and SVÄRDSON (1951) have shown that the hot summer of 1930 caused a strong growth of whitefish (*Coregonus* sp.) in Lake Stora Skeppträsket. SVÄRDSON also pointed out that the hot summer of 1947 caused an unusually high survival of the fry, thus creating a rich year class. In United States BENSON (1953) and COOPER (1953) have found correlations between water temperature, volume of stomach content, growth and condition in brook trout (*Salmo fontinalis* MITCH.). As to the effect of regulations it has already been mentioned above that it often seems to involve an increase in growth during the first years after the start of regulation (RUNNSTRÖM, 1951).

The »condition» is usually expressed by the ratio length: weight. As an example the ratio in fig:s 11 and 12 was plotted in diagrams illustrating the condition of trout and char in September 1949 and 1954 in Lake Blåsjön. The length, however, on the whole being a mathematical function of the weight, it is also possible to express the condition by using the so called FULTON's formula (FULTON 1902):

$$w = \frac{l^3}{100} \cdot c,$$
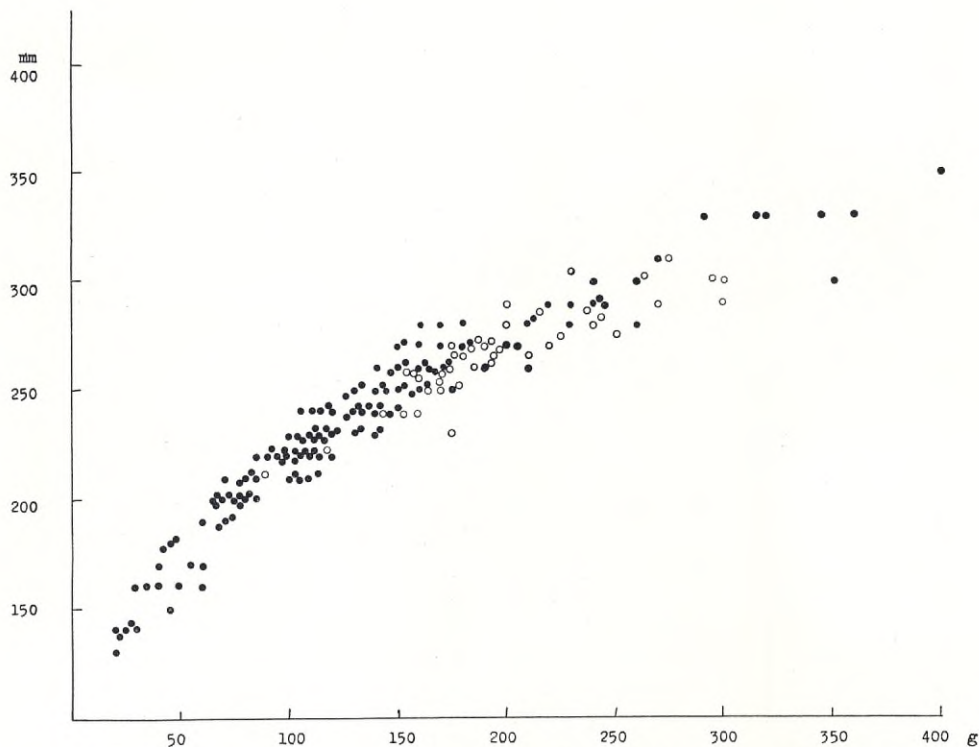
Fig. 11. The ratio length (ordinate): weight (abscissa) during a year of high condition (○=1954) and a year of low condition (●=1949) in trout from Lake Blåsjön.

w representing weight, l length and c a condition coefficient. In order that such an investigation should be relevant the measurements must be very accurate and based on a large amount of material. There are e.g. great differences in weight between wet and dry fishes. There are also differences in growth rate between males and females (ALM 1939).

To illustrate generally the seasonal changes in condition and to support the results from Lake Blåsjön, the condition coefficients of 333 trout and 411 char from Lake Ransaren are given first. The numbers obtained, shown diagramatically in the diagram, fig. 13, show a marked maximum in the summer both in trout and char. The same general trends also characterize the material from Lake Blåsjön, which is given in table 4.

In this lake, however, the condition of both trout and char seem to be much higher. The maximum figure for coefficient of condition also regularly occurs somewhat later than in Lake Ransaren.

The increase in condition in summer may be a response to an optimal water temperature and an abundance of food. The increase in condition is certainly also correlated with an increase in growth rate (cf. BROWN 1946, COOPER 1953, BENSON 1953).
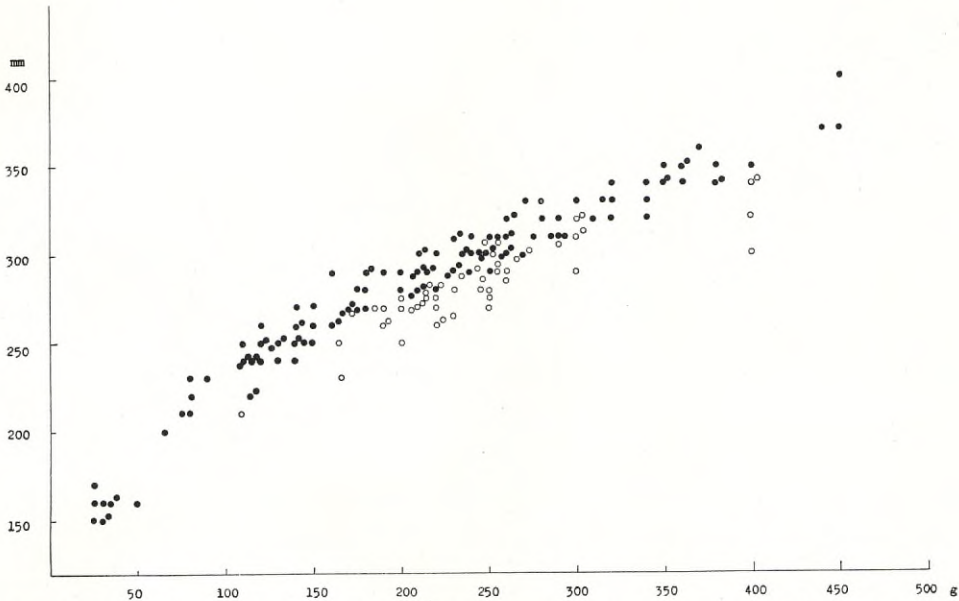
Fig. 12. The ratio length (ordinate): weight (abscissa) during a year of high condition (o = 1954) and a year of low condition (● = 1949) in char from Lake Blåsjön.

Comparing the condition coefficients of the different years under consideration we find that:

1. There are great annual variations in condition, the coefficient being highest in 1954, of decreasing values in 1946, 1945 and 1949 in that order.

2. Both species present the same tendencies though char seem to be more variable in condition than trout (cf. also fig:s 11 and 12).

3. Trout have the highest condition coefficients both in Lake Blåsjön and Lake Ransaren.

As to the two years of 1954 and 1946, characterized by good condition of the fish, it has been stated in the previous chapter that there was certainly also a high organic production in the lake, which may have caused the fish to consume exceptionally large quantities of superabundant and easily available food. In char the consumption of plankton was relatively low. In 1945 and 1949, on other hand, the char's consumption of plankton was very high. In this connection it is of interest to recall DAHL's (1917, 1926) statement that the size of the food objects is of fundamental importance as to the growth of the fish, smaller or less available food objects causing greater exertion to the fish, implying in it's turn a lower growth rate. As it seems probable that the very small planktonic crustaceans may cost the fish more exertion than e.g. *Gammarus* or drowned butterflies the present material strongly supports the statement as well as the fact that char when being the sole inhabitant in a lake (cf. pp. 201—205) prefer other food objects of bigger size. These obser-

Table 4. Condition coefficients of trout and char in Lake Blåsjön.

	Trout					Aver. Aug.–Sept.	Char						Aver. Aug.–Sept.
	May	June	July	Aug.	Sept.		May	June	July	Aug.	Sept.	Oct.	
1945										0.89			0.89
1946			0.88	0.99	1.00	1.00			0.98	0.92	1.01	0.88	0.97
1949		0.93	0.95	0.95	0.95	0.95		0.86	0.85	0.87	0.85		0.86
1954	0.92	0.95	0.93	1.06	1.04	1.05	0.96	0.92	0.92	1.00	1.09	0.91	1.05

vations may also explain the observed fact that trout vary in conditions to a lesser extent than do char, which may be due to their feeding habits being much more conservative than the feeding habits of char. The fact that trout eat much less plankton than do char, also very probably is the reason why trout have the higher coefficient of condition. In Lake Grønningen in Norway SCHMIDT-NIELSEN also reports a lower condition of char during a year with relatively higher consumption of plankton.

Summing up, the condition of the fish seems to depend on the rate of production of the lake and the corresponding amount of reserve food. Plankton is supposed to be less nutritive than other food, thus causing lower condition of the fish, which depend upon it as a principal food item.

Differences in feeding habits between fishes of different size

Table 15 shows the dominating food of the different size groups of fish, as ascertained by the method of calculating the average weight and length of fish using a certain food object as dominating item. To illustrate the problem of interest here, the figures obtained have been arranged in the decreasing order of length (table 5). A very similar table would have been obtained by arranging the fish according to their weight.

Though no measurements have been made of the size of the food objects, a comparison between the food of the bigger and of the smaller fish obviously shows the tendency of bigger fish to consume the bigger food objects (cf. also LINDSTRÖM 1955). Especially marked is the difference between the fish- (and frog-) eating trout and the trout using other food objects.

Availability of the food animals

Comparing the percentage of the different food animals eaten by trout and char and the percentage of the animals in the fauna of the lake, as illustrated by the diagram, fig. 3, it is at once obvious that there are great differences in availability between the different food animals.

The problem of availability has been carefully studied by ALLEN (1941, 1942, 1951) and HESS and SWARTZ (1941), who have expressed the compari-

Table 5. Average length of fish feeding on certain food objects.

	Trout	Aver. length		Char	Aver. length
May	1. Frogs	600		1. *Limnaea* .	340
June	2. Fish	400		2. *Chironom.* p.	295
	3. *Gammarus*	332		3. *Tipulidae* l.	290
	7. Terr. ins.	260		Terr. ins.	290
	8. *Chironom.* p.	253		7. *Ephemeropt.* l.	275
	9. *Chironom.* l.	208		8. *Plecopt.* l.	251
				Gammarus	251
				9. *Chironom.* l.	245
July	1. Fish	340		1. *Limnaea*	405
Aug.	2. *Tipulidae* l.	296		2. *Gammarus*	390
	3. *Trichopt.* l.	275		3. *Pisidae*	385
	9. *Ephem.* l.	225		9. *Phyllopoda*	287
	10. *Eurycercus*	220		10. *Chironom.* p.	270
	Tipulidae i.	220			
	11. Terr. ins.	218		11. *Trichopt.* p.	265
Sept.	1. Spawn	350		1. *Eurycercus*	301
Oct.	2. *Gammarus*	305		2. Spawn	290
	3. *Planorbis*	275		3. *Limnaea*	275
	4. Terr. ins.	257		4. Terr. ins.	274
	5. *Trichopt.* l.	256		5. *Copepoda*	268
	6. *Eurycercus*	250		6. *Phyllopoda*	228

son between food and fauna by calculating the ratio between the percentage of each organism in the stomach of the predator and its percentage in the environment at the same time, which has been called »availability factor» or »forage ratio». A knowledge of the »availability factor» of different food animals in relation to their predators would be of a considerable value in game management or fishery biology, e.g. when trying to estimate if an environment is suitable as biotope for a certain species by taking samples of its fauna.

The samples of the fauna taken in Lake Blåsjön are only by exception suitable to such an investigation.

The term of »availability», when used in this paper, means »the proportion of the population which in a typical habitat would be visible to and of suitable size and taste to be eaten by a fish of the type under consideration» (ALLEN 1941).

Frogs have only been found as winter food of very big trout (cf. Table 5).

Fish (*Salmo* sp.) are to a greater extent consumed by trout than by char. Judging from the material of 1954 mostly big trout have been feeding on fish, which agrees with observations from other Scandinavian lakes (cf. ALM 1939, SCHMIDT-NIELSEN 1939). This is probably applicable to still a greater degree to char (though the only measured char from Lake Blåsjön with fish in its stomach — August 1954 — was only 320 mm in length; the fish consumed, however, in this case was a small fry). In lakes where char regularly feed on fish (Torneträsk, EKMAN 1912, Ladoga JÄÄSKELÄINEN 1921,

Table 6. The percentage of the different species of planktonic crustaceans in Lake Blåsjön in 1949 (from LÖFFLER 1953), and their percentage in the food of char at the same time. L=lake, Ch=char.

	June L	June Ch	July L	July Ch	Aug. L	Aug. Ch	Sept. L	Sept. Ch	Oct. Ch
Eurycercus					—	27	—	10	15
Holopedium	< 1	—	1	6	5	13	16	11	78
Daphnia	< 1	—	2	20	4	17	3	51	3
Bosmina	< 1	—	3	67	74	32	5	9	< 1
Polyphemus			< 1	—	2	—			
Bythotrephes			—	7	—	6	—	4	1
Heterocope					4	5	1	15	4
Diaptomus ssp. ...					< 1	—	< 1	—	
Cyclops	< 1	+	90	< 1	10	—	74	< 1	
Larvae	99	—	3	—	1	—			
Percentage sum ...	100	—	100	100	100	100	100	100	100

Vättern, ALM 1934) the average size of the char is bigger than in Lake Blåsjön. (Cf. also pp. 201—205).

Spawn is regularly eaten both by trout and char during their spawning season in September—October. Judging from the material of 1954 spawn is consumed to the same extent by both sexes. This probably in most cases occurs in direct conjunction with the spawning act, as was observed by FABRICIUS and GUSTAFSON (1954) on char spawning in aquaria.

The crustacean plankton and its importance as food of char has been dealt with above and has also been emphasized by earlier authors (cf. e.g. LINDSTRÖM 1947, 1955, FROST 1951). LÖFFLER's investigation which was partly carried out in connection with the sampling of char stomachs, gives an opportunity to estimate the availability of the different crustacean species. Comparing the percentage of the different species of crustacean plankton in Lake Blåsjön in 1949 and their percentage in the food of char during the same time we obtain table 6.

Though too much value should not be attached to the significance of the figures obtained two facts are clear from the table:

1. High production of a food species is connected with high consumption of the same species. (This becomes more obvious by ignoring the forms *not* eaten — *Cyclops* and larvae — in the table.)

2. Some species, however, are more available than others *Bythotrephes* and *Eurycercus* seem to be extraordinary available, *Holopedium, Daphnia, Bosmina,* and *Heterocope* also show a high degree of availability, while *Cyclops* and the larval forms have a very little availability or no availability at all.

The high availability of *Bythotrephes* and *Eurycercus* may depend on their size, being the two biggest of all planktonic crustacean species found in Lake Blåsjön. The half bentic life of *Eurycercus* may also have been the reason
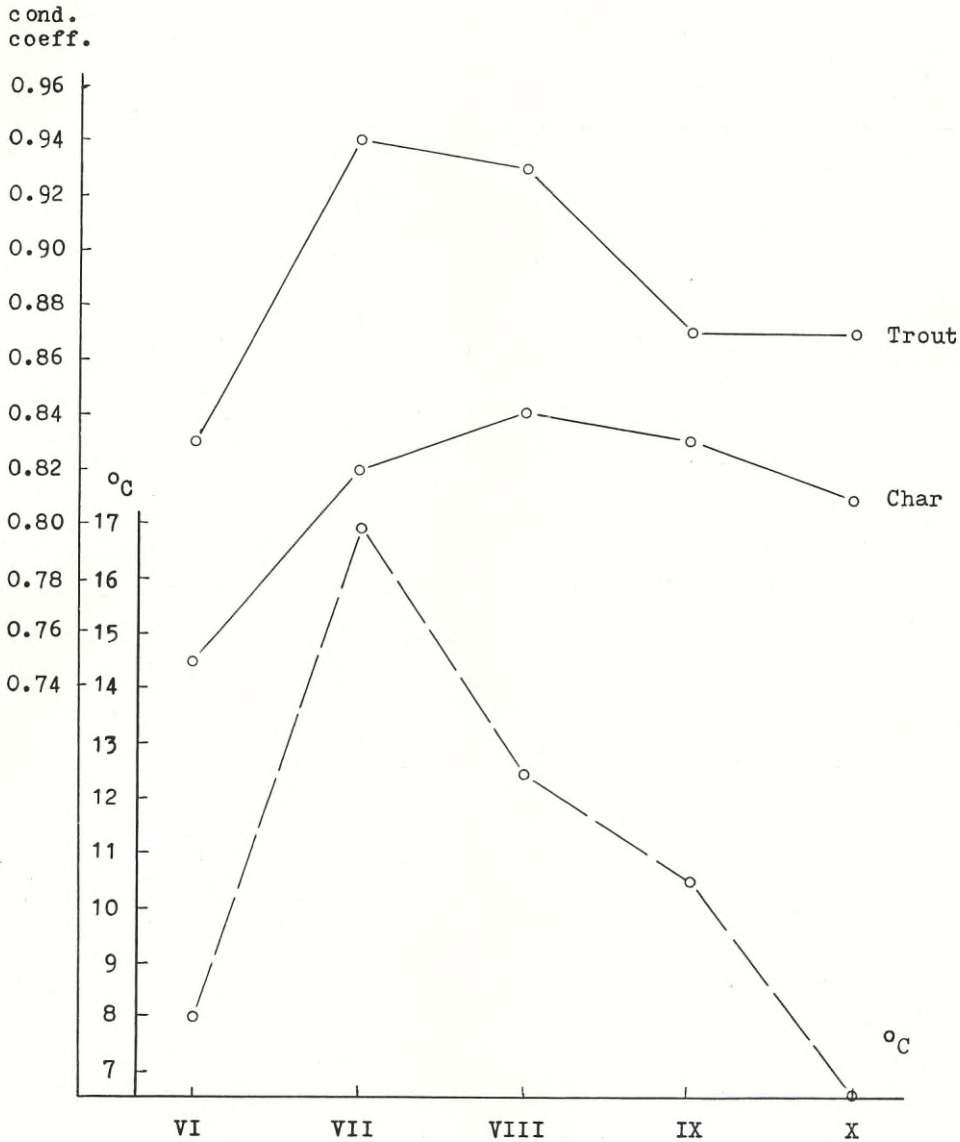
Fig. 13. Seasonal changes in the condition of trout and char in Lake Ransaren, and the mean surface water temperature.

that Löffler did not get it in his net samples. The very low availability of *Cyclops* to *Salmonidæ,* already observed by Southern (1933) and Lindström (1947, 1955), may be due to some quality in *Cyclops* (inconspicuousness, lack of swarm formation, way of moving) which makes it less available than other planktonic crustaceans when present (Cf. Lindström 1955.). So *Cyclops* was found in considerable quantities in stomachs of char caught in the

winter (April 1954), which shows that *Cyclops* in absence of other planktonic crustaceans can have a certain availability. The larvae are certainly too small to be observed by the fish. (For more thourough discussions on the availability of plankton cf. RICKER 1937 and LINDSTRÖM 1955.)

Gammarus lacustris is of great importance as food both of trout and char, constituting the major food item especially of char in winter and spring.

Mollusca (*Limnœa, Planorbis* and *Pisidium*) appear to be little available by comparing their occurrence in the fish stomachs with their very high abundance in the bottom fauna as shown by the diagram, fig. 3. It may, however, be pointed out that *Mollusca* are mostly eaten by relatively big fishes (cf. table 20), which consume relatively more food per individual than do small fishes, a thing that is not clear from the tables.

Oligochaeta, constituting one of the three most abundant groups of the bottom fauna (cf. diagram, fig. 3) are very little available. Bigger earth-worm-like species are to a certain extent consumed especially by char. The very low availability of *Oligochaeta* to *Salmonidae* has also been observed by ALLEN (1941), who explains it by the fact that they are essentially burrowing animals, very rarely visible to the fish.

Trichoptera-larvae (mostly various species of *Limnophilidæ*) constitute the major food of trout during all seasons. This very characteristic trend in the feeding habits of trout in Lake Blåsjön also seems to be valid for other Scandinavian lakes and streams (cf. DAHL 1932, HUITFELDT-KAAS 1935, BRUNDIN 1942, MÜLLER 1954 a). The *Trichoptera*-larvae are of relatively little importance to char.

Ephemeroptera- and *Plecoptera-larvae* are relatively important food both of trout and char.

Coleoptera-larvae (mostly *Dytiscidae*) seem to be more available to trout than to char, but they never constitute any important part of the food of either of them.

Chironomid-larvae, being the most abundant of all bottom animals, play an important part especially in the winter food of both trout and char, though their importance as food is out of proportion to their abundance in the lake. The low availability may depend on the fact that most of the abundant species are burrowing or tube living. It is, however, characteristic that their frequency as occasional food (in very small quantities) is high during all seasons (cf. column F in the tables 11 and 12). If comparing the percentage of the different genera living at the bottom with their occurrence in the fish stomachs we obtain table 7.

It is clear from the table that all species of *Chironomidae* are not equally available, the vivid predatory forms (e.g. *Procladius Paracladopelma, Ablabesmyia, Parakiefferiella, Parachironomus, Macropelopia, Culicoides*) being more available than the sessile forms (e.g. *Paratanytarsus, Tanytarsus* s. str.,
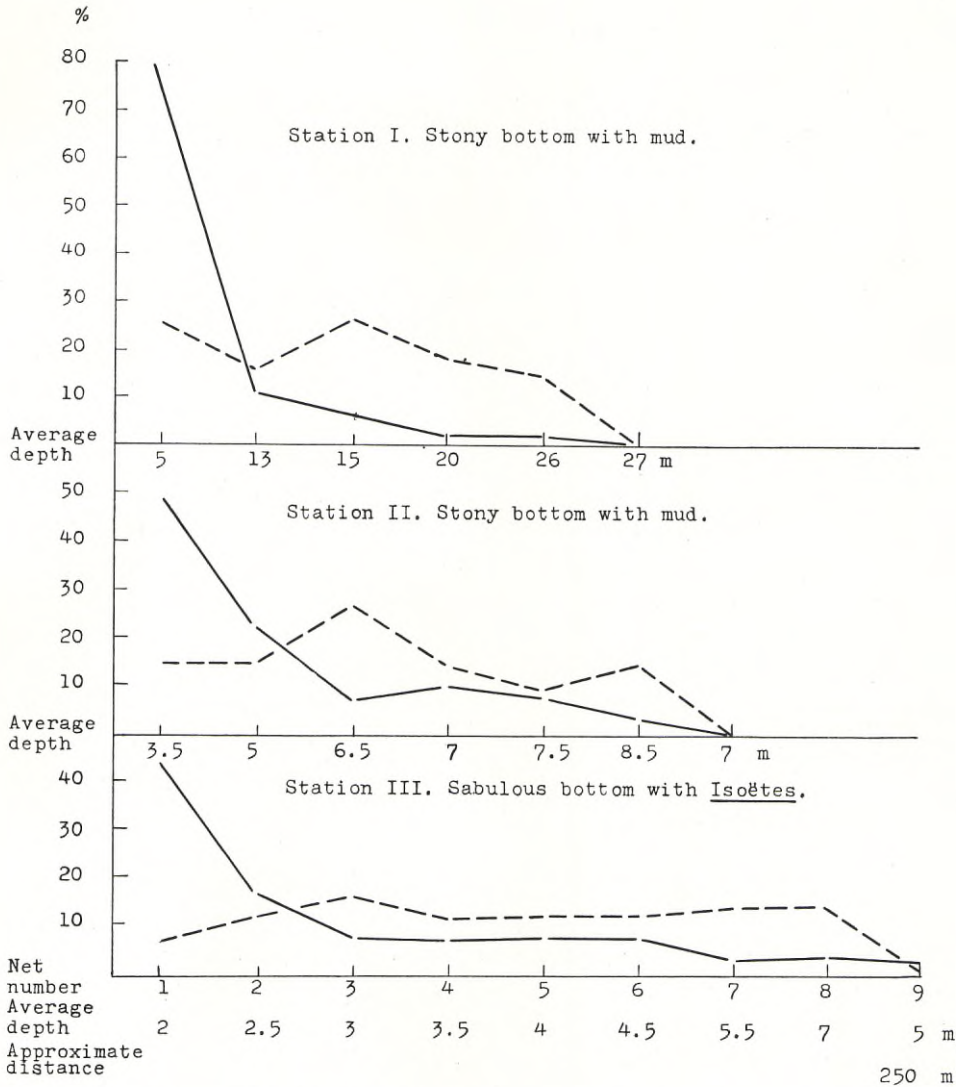
Fig. 14. The percentage distribution of trout (——) and char (— —) in Lake Ransaren, calculated per net length.

Microspectra). The bigger forms (e.g. *Protanypus, Chironomus, Sergentia*) are also more available than the smaller ones.

Simuliid-larvae occur in very small quantities as food of both trout and char, though not belonging to the ordinary fauna of the lake. This may be associated with the phenomenon named »organic drift» (MÜLLER 1954 b), which means the continous stream of more or less bentic organisms occurring in running waters, and probably also in the mouths of the streams.

Table 7. The percentage of chironomid-larvae in the littoral region of Lake Blåsjön (modified after BRUNDIN 1949) and their frequency as fish food, calculated as percentage of fish examined.

	Lake	Trout 1949	Trout 1954	Char 1949	Char 1954
Heterotrissocladius	33	11	10	15	19
Paratanytarsus	13	1		< 1	4
Psectrocladius	11	10	20	13	8
Tanytarsus s. str.	8	1	6		5
Procladius	6	14	10	9	13
Paratrichocladius	6			1	4
Microspectra	5	1			
Monodiamesa	4	2		1	3
Paracladopelma	3	10	2	12	1
Ablabesmyia	2	9	8	15	8
Trichocladius	2	7		1	
Orthocladius	1			< 1	
Parakiefferiella	1	2		18	6
Protanypus	< 1	2	4		3
Limnochironomus	< 1			< 1	
Polypedilum	< 1	2			1
Microtendipes	< 1			< 1	
Parachironomus	< 1	4		2	2
Stictochironomus	< 1	1			
Macropelopia	+	6	2	4	1
Psectrotanypus	+			< 1	
Eucricotopus	+			2	
Chironomus s. str.	+	1	4	1	
Endochironomus	+			< 1	1
Sergentia	+	1	28	1	23
Cryptochironomus s. str.	+	4		1	
Culicoides	+	11	2	3	

Tipulid-larvae constitute an important food of trout, but seem to be less available to char.

Coleoptera-imagines (mostly *Dytiscidae*) have only been found as food of trout, and then in very small quantities.

Chironomid-pupae and -imagines constitute one of the main food items both of trout and char, much more important than e.g. *Trichoptera*-pupae and imagines. The chironomids eaten mostly belong to the dominant genera of *Heterotrissocladius, Psectrocladius, Tanytarsus, Microspectra, Procladius, Ablabesmyia* and others, but more rare species of big size (e.g. *Chironomus anthracinus*) have also occasionally been found in great quantities.

The importance of *terrestrial insects* has already been dealt with in previous chapters. Here only a collation of the taxonomical composition of the insects consumed, as far as it has been possible to identify them, will be given in Table 8.

The table clearly demonstrates a very variable composition of terrestrial

Table 8. Terrestrial insects (and *Araneae*) consumed by trout and char in Lake Blåsjön, calculated as percentage of fish examined.

	Trout			Char		
	1946	1949	1954	1946	1949	1954
Diptera:						
Muscidae		2.0			2.0	
Phoridae		2.0			8.0	
Empididae		19.6	3.8		12.0	
Fungivoridae		3.9			12.0	2.0
Lycoridae		2.0			6.0	
Bibionidae		23.5	1.3		38.0	
Unidentified	81.4	41.2	24.1	39.6	16.0	30.0
Lepidoptera:						
Geometridae			50.6			60.0
(Oporinia)						
Unidentified	12.7			15.1	2.0	
Coleoptera:						
Staphylinidae	12.8	23.5	20.3	1.9	42.0	2.0
Cantharidae	1.2	2.0			8.0	2.0
Coccinellidae			1.3		2.0	
Elateridae	9.3	2.0	1.3	7.5	6.0	2.0
Scarabaeidae			1.3		2.0	2.0
Cerambycidae			1.3		2.0	
Chrysomelidae		7.8	1.3		12.0	2.0
Curculionidae		3.9	3.8			
Ipidae					12.0	4.0
Carabidae	10.5	19.6			4.0	2.0
Unidentified	18.6		2.5	5.7	8.0	12.0
Hymenoptera:						
Tenthredinidae	1.2	5.9			8.0	8.0
Ichneumonidae	44.2	45.1	15.2	26.4	34.0	12.0
Cynipidae		5.9			20.0	2.0
Chalcididae		3.9			2.0	
Formicidae	8.1	11.8	8.9	3.8	16.0	4.0
Sphegidae					2.0	
Apidae	5.8		1.3			
Unidentified	2.3	9.8	3.8		6.0	4.0
Heteroptera:						
Unidentified	1.2				6.0	
Homoptera:						
Cercopidae		2.0			2.0	2.0
Jassidae	9.3	7.8	31.6	11.3	8.0	2.0
Psyllidae		2.0	5.1		2.0	
Aphididae			6.3		4.0	
Araneae:						
Unidentified	2.3	17.6			14.0	

insects from year to year, though the three orders of *Diptera*, *Coleoptera* and *Hymenoptera* always present the most important part. *Staphylinidae* and *Ichneumonidae* have been found in great quantities all years under investigation both in trout and char.

4. **Competition and Ecological Niches in Trout and Char**

General survey of the problem

MAYR (1951) has defined a species as »an aggregate of interbreeding natural populations which are not only reproductively isolated from other such aggregates but also ecologically specialized sufficiently so as not to compete [1] with other such species». This definition gives expression to the fundamental significance of habitat and ecology of the organisms in species-formation.

When two closely related species, after geographical isolation involving genetical reconstruction so as to reach species level, come together again in the range of the parental population, three general types of results are possible:

1. If the change of genetical make-up includes factors for reproductive isolation but not for ecological compatibility, the two species become competitive which leads to the elimination of one species from the area. In different environments and under different climatic circumstances sometimes the one, sometimes the other species will be eliminated, depending upon which species is favored by the existing conditions (cf. PARK 1954).

This principle has been most neatly demonstrated in the laboratory on protozoans (GAUSE 1934) flour beetles (*Tribolium*) (PARK 1948, 1954), *Daphnidae* (FRANK 1952) and *Drosophila* (MOORE 1952, RIZKI *et. al.* 1953).

CLEMENTS and SHELFORD (1939) have defined competition as »a more or less active demand in excess of the immediate supply of material or condition on the part of two or more organisms», which gives expression to the idea that competition may involve many different factors, as space, supply of food, light etc. In the case of big animals such as fish the supply of food may be of fundamental significance (cf. LACK 1954).

2. If the change of genetical make-up includes factors for ecological compatibility, the two species are able to coexist without severe competition, which means that they inhabit different types of habitat or obtain their food or other necessities in a different way; they occupy different ecological niches (cf. GAUSE 1934, LACK 1944, 1946, 1947, 1954, MAYR 1948, 1951).

The general applicability of this principle is most accurately demonstrated in the field with birds. It has been shown that the limits of the niches are often broken down when food objects suitable for two or more species are temporarily super-abundant (LACK 1946, 1947, HARTLEY 1953). It has also

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[1] It may be observed that the term competition here is used in a very narrow sense, expressing a competition resulting in the elimination of one species from the area (point 1. below). When used elsewhere in this paper competition will mean an interaction between individuals of the same species (intraspecific) or between two or more species populations (interspecific), which adversely affects the individual growth and survival or the growth, survival or standing crop of the species populations under consideration (cf. ODUM 1953, CARLANDER 1955).

been pointed out that in places where one species is absent another often expands into its niche (LACK 1947, LACK and SOUTHERN 1949).

3. If the two species are different in size one could become predatory on the other. In that case the prey will either be eliminated, or the two species may live in the area in equlibrium.

This case has been very little studied as to related species. It has, however, been known long that salmonid fishes, for example, could be predatory on each other.

It is yet to be shown that ecological niches also exist in fish, though the definition of niches in fish may as a rule be somewhat more complicated than in birds. In birds the young are fed by their parents, and when grown up their size is limited. In fish the size is extraordinarily variable, young fish as a rule being of smaller size than older ones. The abundance of the different year-classes, however, also affect the growth of the fish so that a high density causes a low growth rate, a low density a high growth rate. So between the different year-classes representing different sizes, there may exist complex interactions. The existance of an interspecific competition causing the elimination of younger year-classes by an older, stronger one has been demonstrated on herring (*Clupea*) (HJORT 1926) and on whitefish (*Coregonus*) (SVÄRDSON 1954 a). A mechanism preventing competition between the year-classes becoming too strong may, however, exist in the fact that bigger fishes as a rule prefer bigger food objects than do smaller fishes. These complicated intraspecific relations may, however, also complicate the relations of one fish species to another, which may make it difficult to give general definitions of their ecological niches, a strong temporal and spatial plasticity being expected. An excellent example of such plasticity is provided by the genus *Coregonus* in Sweden (cf. SVÄRDSON 1954 c).

The term competition has often been used in the literature of fishery biology (cf. e.g. SCHMIDT-NIELSEN 1939, FROST 1946, HARTLEY 1948, MÜLLER 1952), often, however, in a very wide sense as an expression of the fact that different species of fish to a certain extent consume the same sort of food, though their feeding habits never are identical. In Swedish running waters a demonstration of the ecological niches of grayling (*Thymallus thymallus* L.) and trout has been made (MÜLLER 1954 a), showing differences both in their feeding habits and habitats.

Trout and char immigrated into Scandinavia after the end of the last glaciation, and may both belong to the very first members of the Scandinavian fish fauna (EKMAN 1922). They now possess a rather similar distribution, often involving their inhabiting the same lakes. How commonly this is the case is clearly shown by table 9. Of 46 lakes in the northern part of Jämtland (including Lake Blåsjön) 20 are inhabited by both trout and char, and the most common type of fish community is that of »trout-char» (17 lakes).

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Table 9. Fish communities in 46 lakes in the northern part of Jämtland.

Perca fluviatilis		+	+	+	+	+	+		+	+	+	+	+	+	+	+		
Cottus gobio						+												
Lota lota			+	+	+	+	+	+	+	+	+	+	+			+	+	
Esox lucius		+			+	+			+	+				+				
Anguilla anguilla						+			+	+								
Phoxinus phoxinus						+			+									
Leuciscus rutilus		+	+	+	+	+	+		+	+						+		
Leuciscus idus																+		
Coregonus sp.		+		+		+	+		+	+	+	+				+		
Thymallus thymallus ..						+	+		+	+	+							
Salmo alpinus	+					+	+	+						+				
Salmo trutta	+	+					+	+	+	+	+	+	+	+				
Number of lakes	17	8	3	3	2	2	1	1	1	1	1	1	1	1	1	1	1	Sum 46

This example certainly could be multiplied several times in all the arctic-boreal (EKMAN 1922) part of Scandinavia.

As both species spontaneously occur in the same sorts of waters it is to be expected that they should have essential similarities in ecological demands, but also that they should possess different ecological niches. The most striking and best known difference in ecology is that of their spawning habits, trout always spawning in running waters, char as a rule in lakes (cf. FABRICIUS 1950, 1953 a). It is also a wellknown fact that trout regularly occur in running waters also out of the spawning time, but char only exceptionally.

As to the feeding behaviour, FABRICIUS (1953b) has pointed out some essential differences: »Contrary to the trout the char does not usually hide between or under stones. — When hunting for food objects floating in the water, the char swims about for a long while, swallowing a large number of these objects in rapid succession. In this behaviour the char differs from the brown trout which usually makes a sudden forward dash, snapping up a food object and then immediately turns round returning to its cover on the bottom.» These observations in general indicate a more territorial behaviour in trout than in char, which may be due to an adaptation more to running than to stagnant water.

Regarding the possibility of competition between trout and char it has been stated in Scandinavian literature (DAHL 1920, ALM 1935, SCHMIDT-NIELSEN 1939) that char, if introduced into trout lakes very often ruins the trout population. It has also been shown (SVÄRDSON 1949 a) that char if being kept in troughs and being given only the same sort of food as trout, tend to eliminate the latter.

In the following chapters the competition between trout and char will be discussed on the basis of the present material.

Competition for space

The important fact that trout spawn in running water, while char, as a rule, spawn in stagnant water generally exclude competition for spawning

ground. This also prevents hybridization and competition for food during the delicate earliest stages of the fish.

Using a popular analogy the habitat of an animal is its »address» and the niche its »profession» (ODUM 1953). As, however, one is unlikely to find a shoemaker in a tailors shop, so different niches may also involve slight differences in the choice of habitat in animals. It has also been shown that e.g. different species of titmice (*Parus*) in some cases use different parts of the same trees (HARTLEY 1953). In running waters grayling (*Thymallus*) occupies bottom regions in the middle of the stream, trout regions with open, slowly running water (MÜLLER 1954 a).

The test-fishing-method mentioned at page 164 offered the possibility to study the differences in distribution between trout and char in Lake Ransaren. The diagram, fig. 14, shows the percentage distribution of the catch of trout and char in Lake Ransaren, calculated per net length counting from the shore towards the centre of the lake at three different fishing stations. Though there are also slight seasonal differences within the species, there is a characteristic difference in distribution between the two species during the summer season involving trout inhabiting mainly the shallow, interior parts of the littoral region, char inhabiting the deeper exterior parts.

To what extent this difference in distribution depend mainly on competition or to what extent some other factors are involved, is a difficult problem to solve without careful investigations in lakes where each species is the only inhabitant. The fact, however, that the pictures obtained at all three stations are so similar, in spite of the physical conditions of their bottoms being very dissimilar (station I having a very steep, stony bottom; station III a very flat bottom, overgrown with *Isoëtes*), indicates that specific interactions are at work. It has also been observed that, in lakes only inhabited by trout or by char, the population has a more even distribution all over the lake (FABRICIUS 1953 a).

The fact that trout is mainly a bottom feeder with very strong territorial instincts, while animals floating in open water are more available to char than to trout, may explain why trout is the species occupying the shallow parts of the littoral region. This, however, may not necessarily indicate that open, deep water offers the optimal habitat of the individual char.

Competition for food

It has already been pointed out in previous chapters that there are considerable differences between the feeding habits of trout and char, the most obvious one being that in summer trout feed on bottom animals (above all *Trichoptera*-larvae), char on planktonic crustaceans.

Here the three years from which complete samples are available will be examined once more; this time from the view-point of the problem of compe-
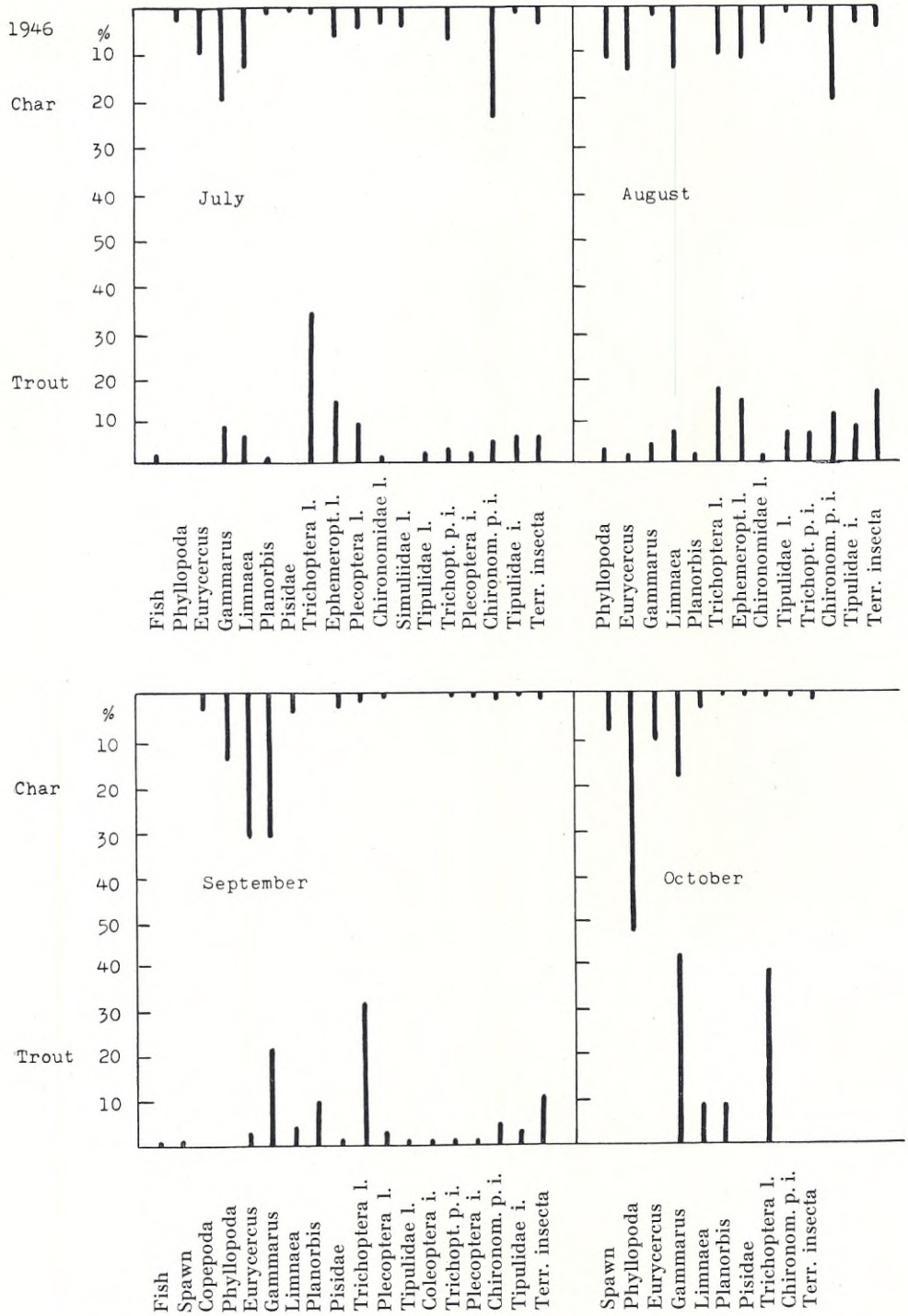
Fig. 15. The food of trout and char in Lake Blåsjön. July—October 1946.
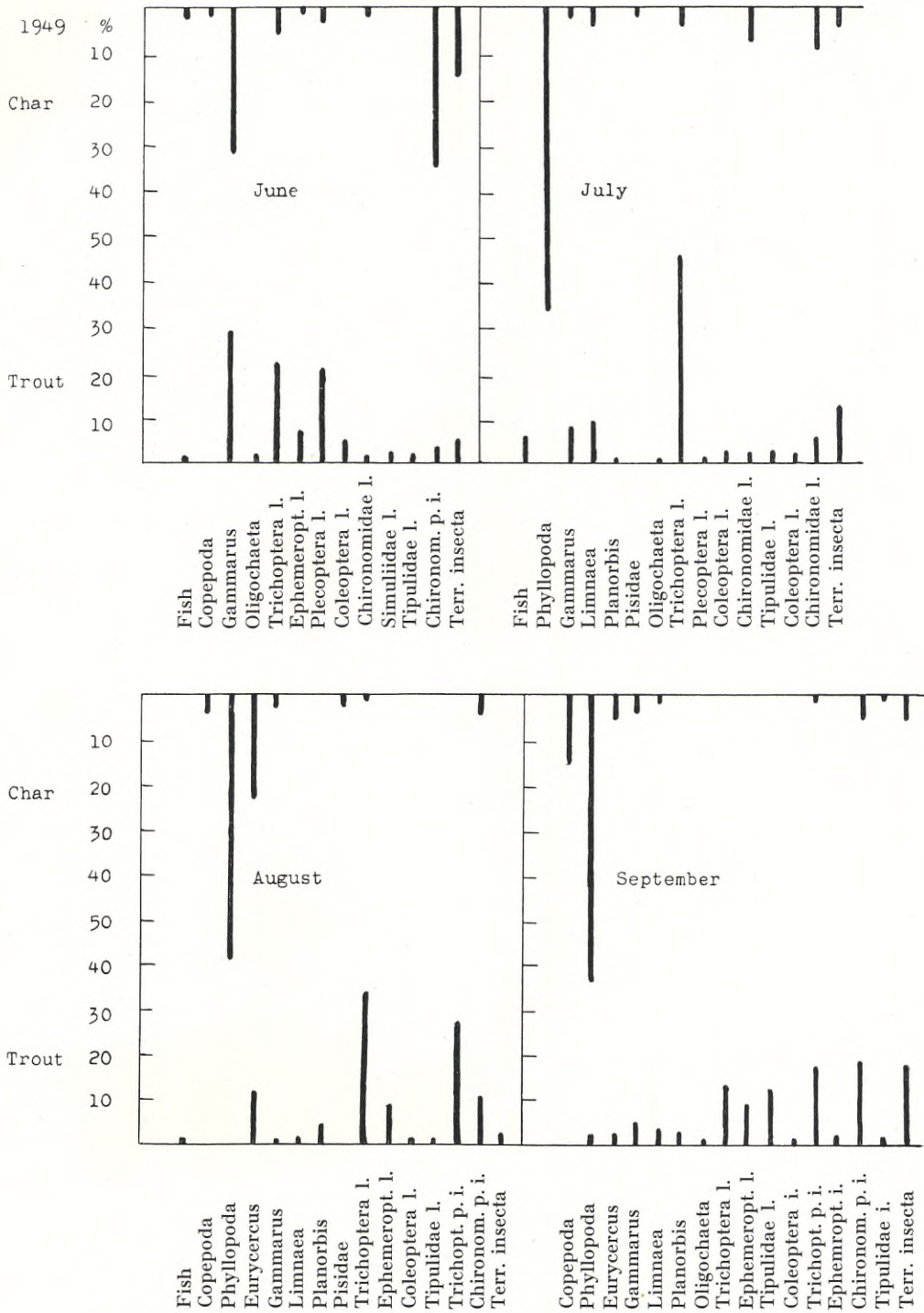
Fig. 16. The food of trout and char in Lake Blåsjön. June—September 1949.
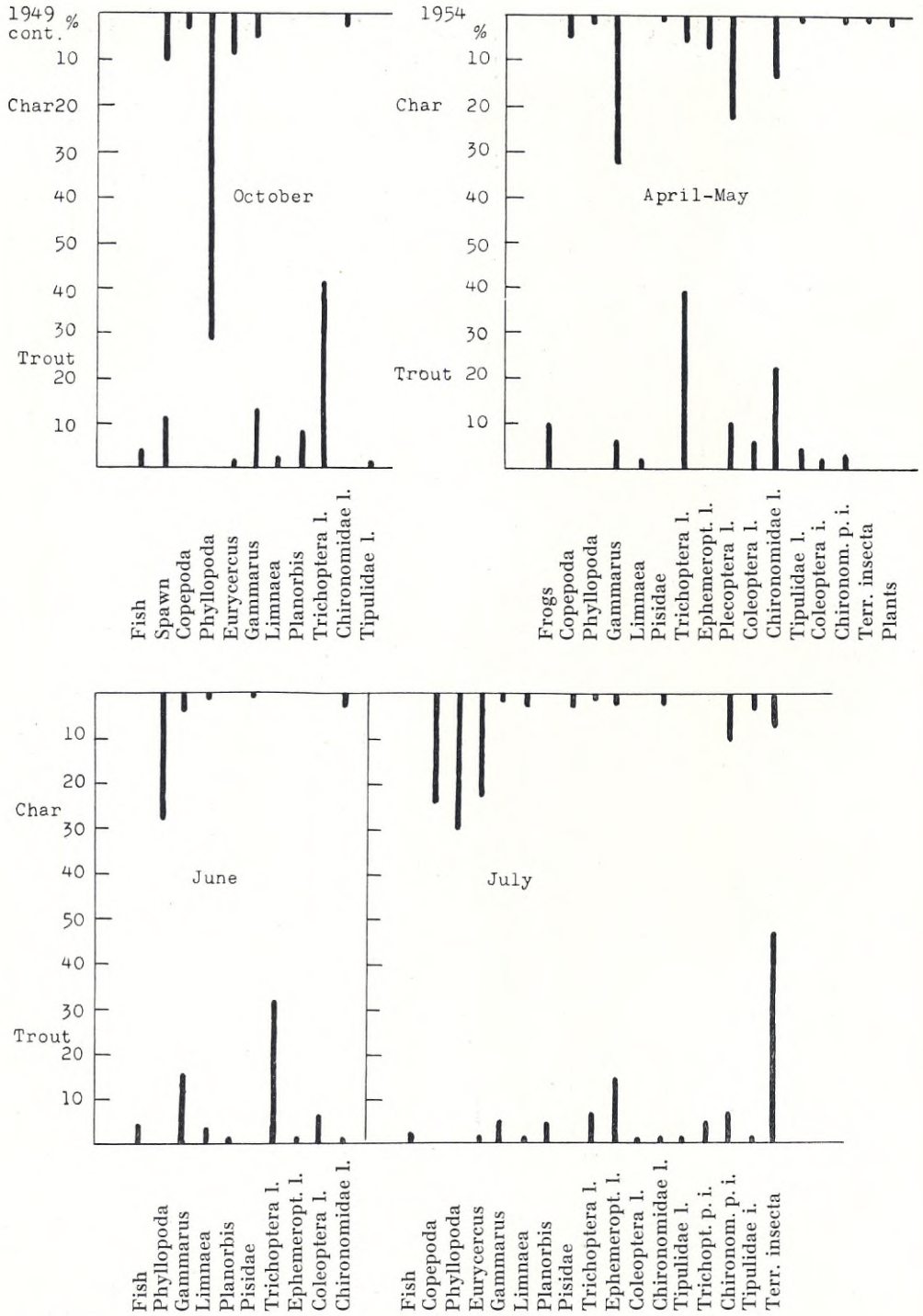
Fig. 17. The food of trout and char in Lake Blåsjön. October 1949 and April—July 1954.
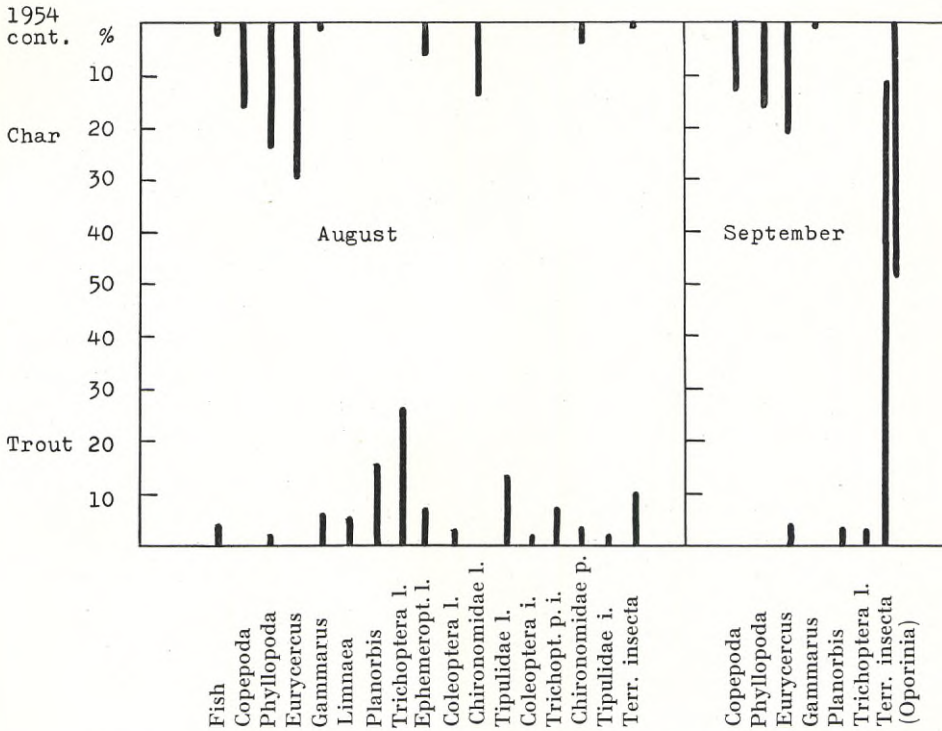
Fig. 18. The food of trout and char in Lake Blåsjön. August—September 1954.

tition. The diagrams, fig:s 15, 16, 17 and 18, illustrate the feeding habits of trout and char during the years 1946, 1949 and 1954 in a way to make it possible to study the differences between the two species.

1946. Already in July the differences in feeding habits were vague, both species feeding on bottom animals and hatching insects. The breakdown of the limits of the niches was complete in August, no significant differences in feeding habits being noticeable. In September a rebuilding of the niches started, involving the characteristic feeding on *Trichoptera*-larvae by trout, on plankton by char. The niches were still more marked in October. *Gammarus,* however, was consumed to a great extent both by trout and char in September as in October.

Without knowledge of the feeding habits in other years and the possible variations in the production of food in the lake, one would certainly interpret the picture obtained of the feeding habits as indicating considerable competition, the food of the two species during the time of their strongest growth being nearly alike. As has been pointed out in the previous chapter, however, there are reasons for presuming that the organic production in the lake this year was very high, a presumption that is well supported by the fact that the condition of the fish this year was very high. The obvious breakdown of

the limits of the niches because of that may be interpreted as a cause of superabundance of food (above all *Gammarus*), which means that the two species could feed on the same food without competing.

1949. The niches this year were already very well defined in spring, the only organism being used by both species to an extent worth mentioning being *Gammarus*. This, however, occurred at a time of its highest abundance in June.

As mentioned in the previous chapter there are reasons for presuming that the organic production of the lake this year was low which is well supported by the low condition of the fish. Thus competition, so it seems, forced the two species into their niches. Being the species with the strongest territorial instincts, it seems natural that trout had the best qualifications to occupy and defend the internal parts of the littoral region housing the food tempting to both species.

1954. This year also the niches of the two species were already well defined from the beginning of the summer season. Especially interesting are the conditions during the winter, when only the bottom food is available to both species. A tendency to the formation of »winter-niches» is obviously indicated, involving the trout feeding primarily on *Trichoptera*-larvae and *Chironomidae*-larvae, char on *Gammarus* and *Plecoptera*-larvae.

The general charactere of the niches for the rest in general resembled these of 1949, the importance of the bottom food to trout, however, being less marked and compensated for by insects. In September the mass development of *Oporinia* caused a drastic breakdown of the niches.

It then seems clear that in lakes inhabited by trout and char the fish occupy well defined ecological niches, the most important trend being that char, during the time when the bottom food tempting to both species reaches its lowest abundance, turns to the open waters to feed on plankton. When food tempting to both species is temporarily superabundant the limits of the niches are broken down.

Of fundamental interest in this context is the difference between the optimal conditions of the individuals of a species and the optimal conditions of the species in relation to other species. In general the optimal conditions of the individual may be defined as the conditions chosen by the individuals of a species in the absence of other competitive species, or the conditions giving an advantage for one individual over competing individuals of the same species (intraspecific competition). The optimal conditions of the species, on the other hand, are the conditions giving an advantage for one species over competing populations of other species (interspecific competition) (cf. Svärdson 1949 b, Odum 1953). Concerning closely related, sympatric species the individual optimum and the species optimum may very often be very different or antagonistic. For example, big size (to a certain limit) as a rule implies a positive survival value for the individual. The optimal food of the indivi-

dual thus may be the food causing the best growth. Using the present case as an example, the individual char tends to chose food objects that are big or available enough to cause a rapid growth. As to the species, on the other hand, small size in many cases implies a positive survival factor, preventing hybridization and competition between closely related species (SVÄRDSON 1954 b). The genus *Coregonus,* for example, which has five sibling species in Sweden, have very subtle morphological characteres. The size distributions of the species, however, are very divergent when they are living side by side in the same lake (SVÄRDSON 1949 c). This is the cause of the consumption of food particles of different size or availability, and implies differences in ecology, necessary for the species to be able to live side by side without severe competition.

It seems clear from the present investigation that planktonic crustaceans (and open water) implies an optimum for char as species in relation to the competing trout species. The low individual growth rate may in this case be compensated for by a numerous population which can successfully compete with the less numerous trout population (cf. p. 194). For the individual char, however, other food objects and other habitats provide an optimum, which means that char, when bigger and more available food objects can be eaten without competition, turn to these and increase in size and condition.

More light should be shed on this problem after studying the habits and conditions of the two species when being in sole control in a lake. A case where char is the only inhabitant of a lake will be described in the next chapter.

The feeding habits of char in Lake Korsvattnet

As mentioned above only char occur in Lake Korsvattnet. There are, however, two distinct forms of char in the lake, one with a very rapid growth rate (here called »big char»), the other with a very slow growth rate (here called »dwarf char»). The obvious difference in growth rate is evident from the diagram, fig. 19, which is drawn from unpublished data worked out by S. RUNNSTRÖM. It is also evident from the diagram that »big char» attain a greater age than »dwarf char».

The length distributions of the two forms and of the char of Lake Blåsjön are illustrated by the diagram, fig. 20. The fish in both lakes were caught with nets of the mesh sizes of 10, 12, 14, 16, 18, 20, 24, 34, and 40 rows per ell. (»ell» here means the Swedish measure *aln,* which corresponds to 0.59 m). It is obvious that the size of the char of Lake Blåsjön lies between the two but is nearer that of the »big char». As there are also differences in the feeding habits of the two forms, they are treated separately in this paper. When separating them, consideration was taken to their age in relation to the size and the degree of ripeness of their gonads.

In comparing the feeding habits of the »big char» of Lake Korsvattnet (cf.
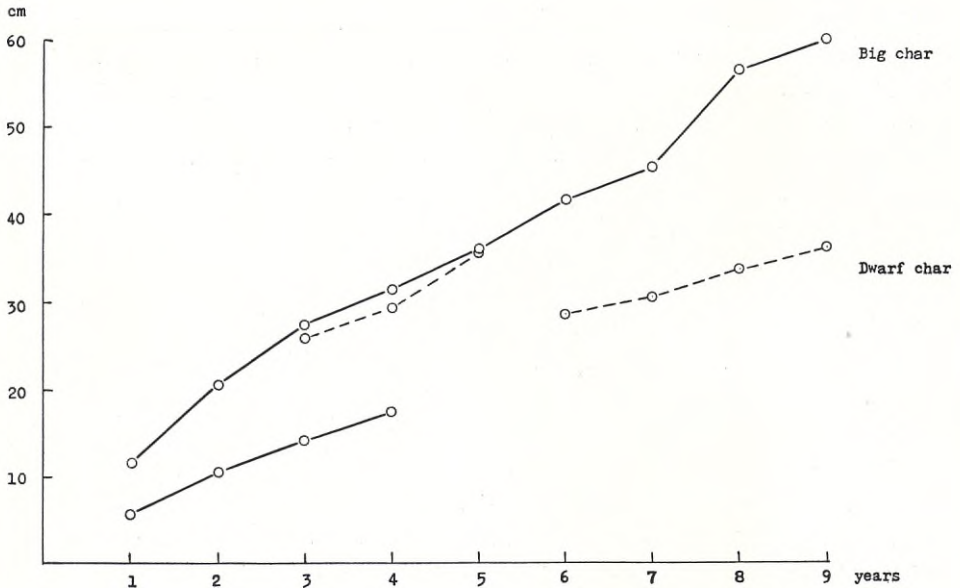
Fig. 19. Growth of the »big char» and the »dwarf char» of Lake Korsvattnet (—) and Lake Kultsjön (- - -). After RUNNSTRÖM (unpublished data) and OLOFSSON (1932 b).

diagram, fig. 21) with those of the char of Lake Blåsjön, we find very important differences:

1. In contrast to the circumstances in Lake Blåsjön, fish (in most cases certainly »dwarf char») are regular and important food of the »big char». This certainly is a result of its big size, which makes it possible for it to be predatory on as big animals as other char (cf. p. 184).

2. Planktonic crustaceans are of very little importance as food of »big char». As the supply of plankton, judging from the food of the »dwarf char» seems to be normal, this fact supports the idea that when char have access to other more available food, they despise plankton.

3. Instead of plankton the predominant food of »big char» in summer consists of hatching and flying insects. This is characteristic for all years under investigation, and may indicate the real optimal food of the individual char. It may, however, be pointed out that Gammarus, which is of extraordinary importance as food of char in Lake Blåsjön, is lacking in the fauna of Lake Korsvattnet.

On the whole it is obvious that the »big char» of Lake Korsvattnet occupy quite a different niche from the char of Lake Blåsjön, a phenomenon that is also correlated with a higher growth rate. It seems very probable to the present author that this is a result of the lack of competition from other fish species.

Turning now to the »dwarf char» its feeding habits are very different from
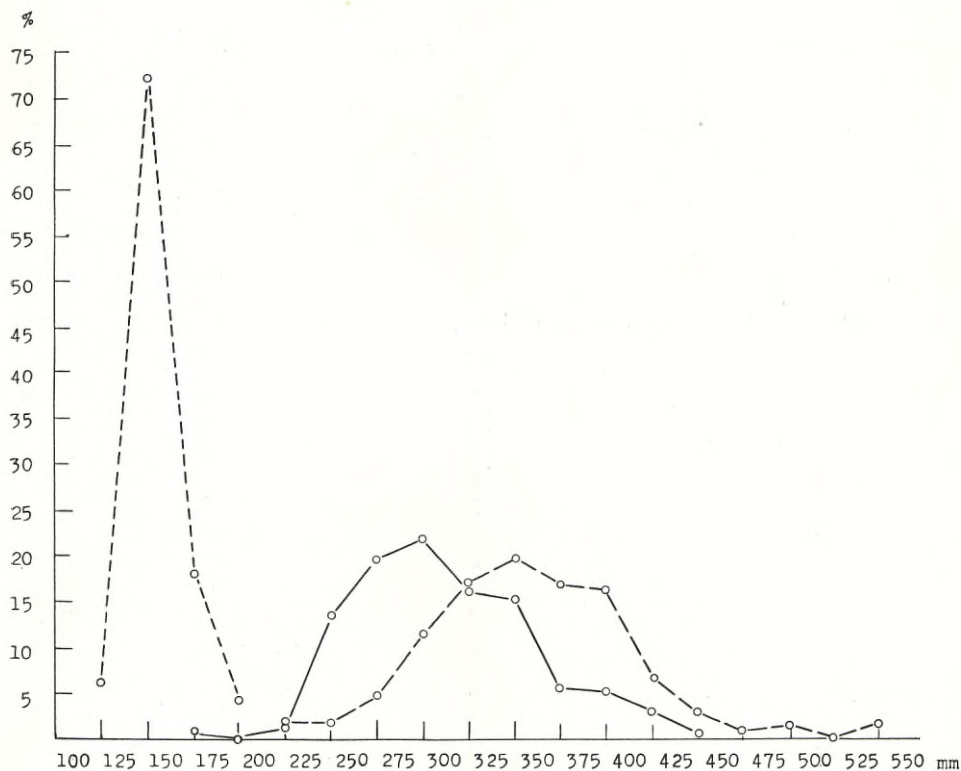
Fig. 20. The length distribution of the char of Lake Blåsjön (——), the »big char» (— —) and the »dwarf char» (– – –) of Lake Korsvattnet.

these of the »big char» (cf. diagram, fig. 22). The niche occupied by the »dwarf char» is characterized by a very extensive consumption of crustacean plankton and seems on the whole very similar to that of the char of Lake Blåsjön. Ecologically the »big char» on the whole seems to correspond to the trout, the »dwarf char» to the char in Lake Blåsjön.

The occurrence of two forms of char in the same lake, with distinctly different ecological niches and different growth rate, creates a problem of great interest, difficult to solve without additional material. It may, however, be mentioned that the phenomenon is strongly reminiscent of the one of »sibling species», as occur for example in *Coregonus* (cf. SVÄRDSON 1949 c). It may also be pointed out that several species of char have been described both in Europe (BERG 1948) and North America (VLADYKOV 1954). VLADYKOV states that *S. alpinus* in Canada consists of two or possibly more species. In Sweden EKMAN (1912) and OLOFSSON (1932 b) have shown that in many lakes (e.g. Lakes Torneträsk, Storuman, Kultsjön, and Ransaren) two forms of char occur, one with a high growth rate the other one with a low growth rate. On material from Lake Kultsjön (near Lake Ransaren, cf. map, fig. 1) OLOFSSON
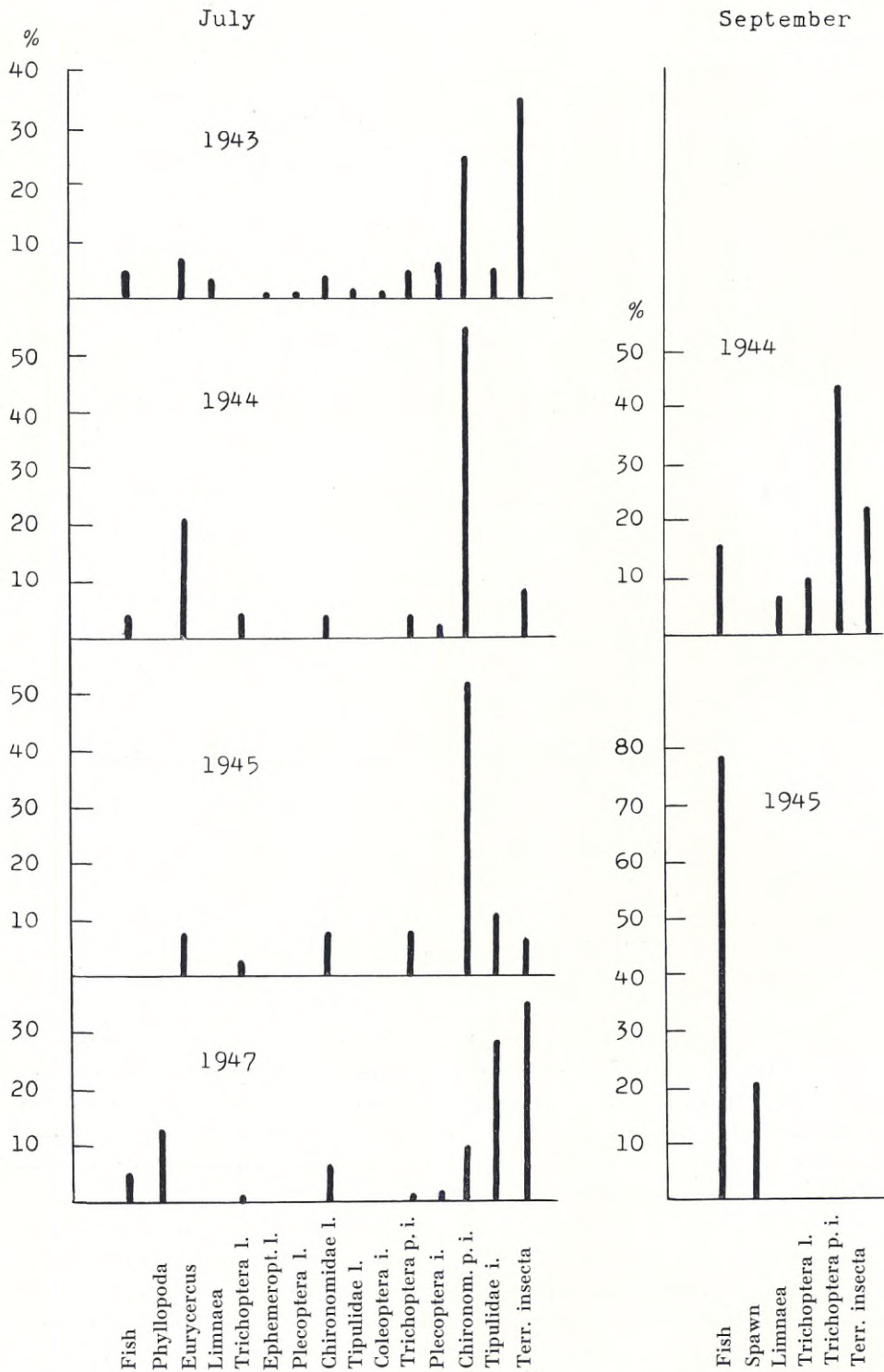
Fig. 21. The food of »big char» in Lake Korsvattnet. July 1943, 1944, 1945, and 1947, September 1944 and 1945.
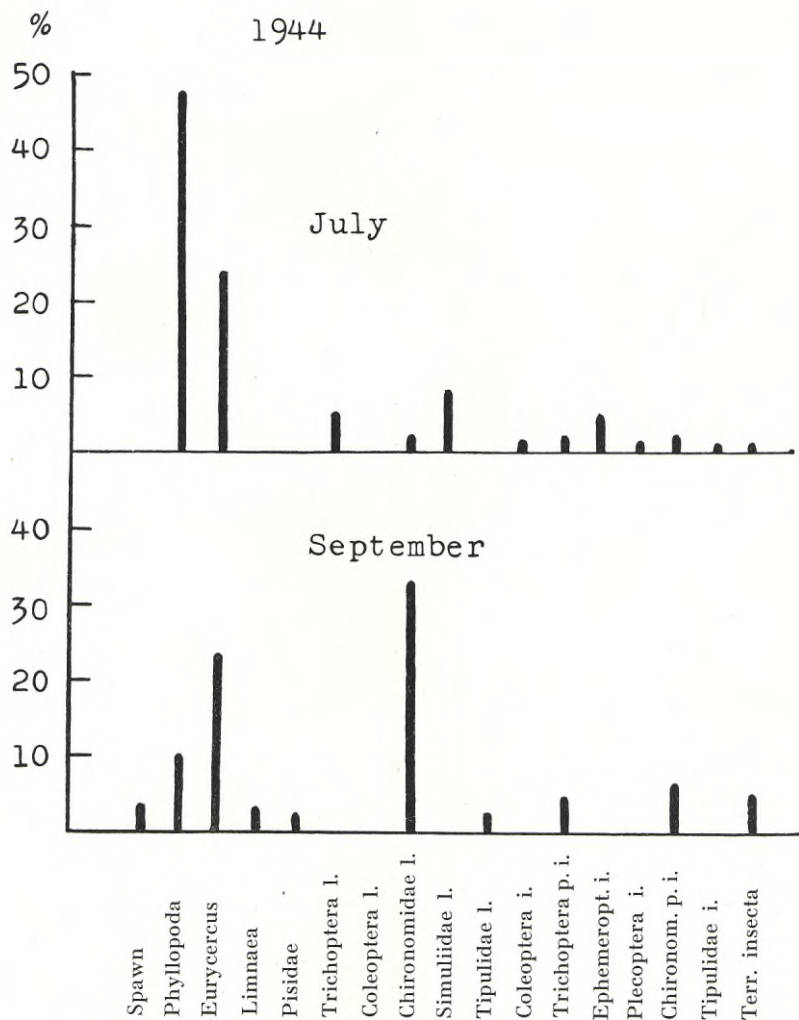
% 1944

Fig. 22. The food of »dwarf char» in Lake Korsvattnet. July and September 1944.

has made calculations of the growth rate of the two forms, the result of which shows good conformities with RUNNSTRÖM's calculations from Lake Korsvattnet (though the »dwarf char» of Lake Kultsjön seems to have a somewhat higher growth rate than that of Lake Korsvattnet. It also attains a much higher age, (cf. diagram, fig. 19). OLOFSSON also pointed out that »dwarf char» as a rule spawn later than »big char».

Similar cases have been reported from other parts of Europe. In Lake Windermere in Great Britain there are three forms of char (FROST 1951). Besides two autumn spawning populations with different growth rates and different size distribution, there is also in this lake a third, spring spawning population. In the alpine lakes of middle Europe several forms of char living

side by side in the same lake, but having different growth rate and different spawning times, have been described (NERESHEIMER 1924, SCHINDLER 1950). Also from Iceland there have been reported a similar case (FRIÐRIKSON 1939, LAMBY 1942). In Lakes Thingvallavatn and Mývatn in Northern Iceland there are two forms of char, one with high growth rate, another, the »krús», of dwarf size. The two forms also have different feeding habits and different distribution in the lakes.

There exist also in Lake Blåsjön a divergent population of char (cf. MÄÄR 1949) with a lower growth rate and differences in spawning habits and habitat distribution. Being very difficult to catch and to distinguish from the »ordinary» char, except during its spawning time, its feeding habits have not yet been studied. It is a priori impossible to know which of the two forms of Lake Korsvattnet and Lake Blåsjön correspond to each other. *Ecologically* the »dwarf char» of Lake Korsvattnet obviously correspond to the bigger char of Lake Blåsjön (the subject of this investigation) but this is no criterium for a *genetical* identity also, as interactions between trout and char must also be taken into consideration. To get nearer the goal of a general definition of the niches of char, a morphological-taxonomical investigation must first be carried out to make clear the possible racial or specific conditions in char.

5. **Summary**

1. About 2,400 trout and char from three lakes in the North Swedish mountain region were examined as to their feeding habits, conditions, and ecological niches.

2. The two species were found to have characteristic seasonal variations in their feeding habits, which, it is suggested, depend on seasonal variations in the abundance of the different food objects in the fauna.

3. It is suggested, annual variations in the feeding habits of the fish depend on variations in the organic production of the lake or other changes in the supply of food animals, e.g. those brought about by lake regulations.

4. Characteristic seasonal variations in the condition of the fish were found. Annual variations in the condition are supposed to depend on variations in the organic production of the lake or other changes in the supply of food animals.

5. Differences were found in the feeding habits of fish of different size. On the whole bigger fish consume bigger food objects.

6. Great variations in the availability of the different food animals were found.

7. The two species were found to have obvious differences in their habitat distribution, trout occupying the inner shallow parts of the littoral region, char the outer, deeper parts.

8. As to the feeding habits of the two species they were found to occupy well defined niches, the most important trend of which is that char, during the time when the bottom food, suitable to both species reaches its lowest abundance, turn to open waters to feed on plankton. When food suitable to both species is temporarily superabundant the limits of the niches are broken down.

9. In a lake in which char are the sole inhabitants, two forms of char were found. A »big char» was found to occupy a niche different from that of char in a »trout-char-lake», characterized by an extensive consumption of fish and hatching and flying insects. A »dwarf char» was found to occupy a niche similar to that of char in a »trout-char-lake».

Acknowledgements

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7. Tables

Table 10. The bottom fauna of Lake Blåsjön. Individuals per m².

Depth m	0—1	1—2	2—4	4—6	6—8	8—10	10—12	12—14	14—16
Tricladida	—	3	7	29	9	—	12	1	8
Nematodes	—	17	86	81	44	96	58	160	47
Hirudinea	—	—	15	—	—	—	—	—	—
Oligochaeta	93	377	380	1,214	688	813	764	629	258
Asellus	—	—	—	2	—	—	—	17	—
Gammarus	—	9	28	31	6	5	7	—	—
Copepoda	—	23	40	7	5	6	9	11	—
Hydracarina	—	6	10	14	5	4	8	1	5
Trichoptera	—	15	16	4	3	3	7	—	5
Plecoptera	—	6	10	5	—	—	—	—	—
Ephemeroptera	—	19	8	1	—	—	—	—	—
Chironomidae	26	601	650	1,153	1,040	788	913	612	235
Mollusca	15	203	214	291	232	157	184	257	106
Miscellaneous	—	—	18	21	7	4	1	8	—
Sum	134	1,279	1,482	2,853	2,039	1,866	1,963	1,696	664

Table 10 (continued).

Depth m	16—18	18—20	22—24	24—26	26—28	30—40	40—50	70—80	100—110
Tricladida	—	—	47	—	—	—	—	—	23
Nematodes	235	47	70	35	164	14	47	12	59
Hirudinea	—	—	—	—	—	—	—	—	—
Oligochaeta	279	69	69	163	116	100	208	81	312
Asellus	—	—	—	—	—	—	—	—	—
Gammarus	—	—	—	—	—	—	—	—	—
Copepoda	47	—	—	23	—	—	—	—	—
Hydracarina	47	—	—	—	—	—	—	—	—
Trichoptera	—	—	—	—	—	—	—	—	—
Plecoptera	—	—	—	—	—	—	—	—	—
Ephemeroptera	—	—	—	—	—	—	—	—	—
Chironomidae	885	186	512	524	494	256	429	427	547
Mollusca	46	—	209	279	163	54	58	—	43
Miscellaneous	—	—	—	—	—	—	—	—	—
Sum	1,539	302	907	1,024	937	424	742	520	984

Table 11. Food of trout. Lake Blåsjön 1944—1954.

l=larvae, p=pupae, i=imagines, plankt.=planktonic, aq.=aquatic, V=volumetric, F=frequency, D=dominance.

Number of fish examined	1944 July 69			1945 August 35			1946 June 6		
	V	F	D	V	F	D	V	F	D
Frogs									
Fish	1.5	2.9	1.7				4.9	16.7	—
Spawn									
Phyllopoda, plankt.	1.5	2.9	1.7	5.4	5.7	5.7			
Eurycercus	0.3	10.1	—	8.1	14.3	8.6			
Gammarus	3.9	30.4	3.3	14.1	28.6	14.3	0.1	16.7	—
Asellus				0.3	2.9	—			
Limnaea	2.6	14.5	3.3	9.0	25.7	8.6			
Planorbis	1.7	11.6	—	4.3	20.0	2.9			
Pisidae	< 0.1	1.5	—	0.1	8.6	—			
Oligochaeta									
Hydracarina	< 0.1	2.9	—						
Trichoptera l.	21.8	58.0	28.3	13.8	40.0	17.1	29.3	66.7	33.3
Ephemeroptera l. ..	6.0	36.2	5.0	9.9	11.4	11.3	9.0	50.0	—
Plecoptera l.	0.8	11.6	—	5.4	11.4	5.7	32.6	100.0	33.3
Megaloptera l.	< 0.1	2.9	—						
Coleoptera l. (aq.) .	1.4	14.5	—	2.9	2.9	2.9	2.0	50.0	—
Chironomidae l. ..	0.2	26.1	—	0.1	20.0	—	8.1	16.7	16.7
Simuliidae l.	0.1	4.3	—						
Tipulidae l.	0.9	5.8	1.7	0.6	2.9	—	2.4	16.7	—
Coleoptera i. (aq.) .									
Trichoptera p. i. ...	4.0	14.5	—	8.0	11.4	5.7			
Ephemeroptera i. ..									
Plecoptera i.				0.3	2.9	—			
Megaloptera i.									
Chironomidae p. i. .	26.3	55.1	25.0	8.6	17.1	8.6	9.8	16.7	16.7
Tipulidae i.	15.0	36.2	16.7						
Terr. insecta	11.9	49.3	13.3	9.1	22.9	8.6	1.8	16.7	—
Miscellaneous									
Percentage sum ...	100.0		100.0	100.0		100.0	100.0		100.0

1946 July 56			1946 August 40			1946 September 94			1946 October 17		
V	F	D	V	F	D	V	F	D	V	F	D
1.7	3.5	3.5				1.1	1.1	1.1			
						0.8	1.1	1.1			
			2.5	7.5	2.5	< 0.1	1.1	—			
			0.6	5.0	—	2.9	13.8	3.2	0.1	5.9	—
7.9	39.3	9.0	3.6	15.0	2.5	22.1	59.6	24.5	42.3	70.6	41.2
5.8	25.0	3.5	7.4	27.5	7.5	4.4	27.7	2.1	9.3	35.3	11.8
0.8	7.1	—	1.7	5.0	2.5	9.7	26.6	10.6	8.8	23.5	5.9
			< 0.1	5.0	—	0.8	11.6	—			
0.3	1.8	—									
< 0.1	1.8	—	< 0.1	5.0	—						
32.7	76.8	37.6	17.0	42.5	17.5	31.7	73.4	37.1	39.1	52.9	41.1
14.4	33.9	16.2	13.7	35.0	12.5	< 0.1	1.1	—			
9.4	35.7	7.1	0.2	15.0	—	2.5	18.1	—	0.2	11.8	—
0.1	1.8	—				0.9	4.3	—			
0.3	10.7	—	0.1	7.5	—	0.1	3.2	—			
0.7	37.5	—	1.5	30.0	—	0.4	8.5	—	0.1	5.9	—
0.1	8.9	—									
2.3	8.9	1.8	5.6	17.5	2.5	0.8	4.3	1.1			
						0.8	13.8	—	< 0.1	5.9	
3.4	23.2	—	7.5	22.5	10.0	1.3	8.5	—			
1.6	3.5	1.8				1.4	5.3	1.1			
			0.4	7.5	—	< 0.1	2.1	—			
5.4	28.6	3.5	11.6	37.5	12.5	5.1	25.5	3.2			
6.2	23.2	8.9	9.2	22.5	7.5	2.5	18.1	2.1			
6.3	53.6	7.1	17.4	50.0	22.5	10.7	37.2	12.8			
0.1	1.8	—									
100.0		100.0	100.0		100.0	100.0		100.0	100.0		100.0

Table 11. Continued.

Number of fish examined	1949 June 37			1949 July 36			1949 August 38		
	V	F	D	V	F	D	V	F	D
Frogs									
Fish	1.2	2.7	2.7	5.2	5.7	5.7	0.8	2.6	—
Spawn									
Phyllopoda, plankt.				0.3	5.7	—	0.1	10.5	—
Eurycercus				0.1	5.7	—	10.5	28.9	10.5
Gammarus	29.2	64.9	27.0	7.7	37.1	11.4	1.3	18.4	—
Asellus									
Limnaea	0.2	8.1	—	9.2	45.7	5.7	0.5	13.2	—
Planorbis	< 0.1	2.7	—	0.9	20.0	—	3.5	13.2	2.6
Pisidae				0.6	5.7	—	< 0.1	2.6	—
Oligochaeta	1.3	2.7	2.7	1.1	8.6	—	< 0.1	2.6	—
Hydracarina				< 0.1	5.7	—	< 0.1	5.3	—
Trichoptera l.	22.4	51.4	24.3	45.8	80.0	54.3	33.9	71.1	42.1
Ephemeroptera l. ..	6.7	35.1	8.1	0.1	11.4	—	9.4	47.4	10.5
Plecoptera l.	21.3	62.2	24.3	1.0	11.4	—	0.1	5.3	—
Megaloptera l.	1.3	2.7	—	0.2	5.7	—			
Coleoptera l. (aq.) .	3.8	40.5	2.7	1.4	20.0	—	1.0	15.8	—
Chironomidae l. ..	0.6	40.5	—	1.5	60.0	—	0.3	26.3	—
Simuliidae l.	1.6	32.4	—						
Tipulidae l.	1.6	21.6	—	2.4	17.1	—	0.8	5.3	—
Coleoptera i. (aq.) .	< 0.1	2.7	—	2.1	22.9	—	0.2	7.9	—
Trichoptera p. i. ..				0.4	8.6	—	26.0	68.4	23.7
Ephemeroptera i. ..									
Plecoptera i.	< 0.1	2.7	—	0.3	8.6	—			
Megaloptera i.				< 0.1	2.8	—			
Chironomidae p. i. .	3.3	29.7	2.7	6.0	31.4	5.7	9.5	50.5	7.9
Tipulidae i.				0.4	5.7	—			
Terr. insecta	5.4	24.3	5.4	13.3	31.4	17.1	1.9	21.1	2.6
Miscellaneous									
Percentage sum ...	100.0		100.0	100.0		100.0	100.0		100.0

1949 September 33			1949 October 28			1954 April—May 27			1954 June 25		
V	F	D	V	F	D	V	F	D	V	F	D
						8.0	7.7	7.7			
0.2	3.0	—	3.5	3.6	3.6				3.6	4.0	4.0
			10.8	10.7	10.7						
2.0	21.2	3.0									
1.6	21.2	—	1.0	32.1	—						
5.1	15.2	3.0	13.1	39.3	14.3	5.6	42.3	7.7	15.3	56.0	16.0
3.0	24.2	3.0	1.7	17.9	—	1.6	15.4	—	2.8	24.0	—
2.8	18.2	3.0	7.8	28.6	7.1	0.1	3.8	—	0.8	12.0	0.8
									< 0.1	4.0	—
0.9	3.0	—									
13.4	48.5	18.2	60.9	96.4	64.3	38.8	69.2	53.8	32.0	72.0	40.0
6.2	33.3	12.1	< 0.1	3.6	—	0.4	3.8	—	1.0	8.0	—
						10.2	34.6	7.7	< 0.1	4.0	—
						0.4	3.8	—	0.2	4.0	—
0.5	27.3	—	0.1	7.1	—	5.2	19.2	3.8	5.4	24.0	4.0
0.1	9.1	—	0.2	21.4	—	22.5	84.6	15.5	0.6	40.0	—
11.9	33.3	12.1	0.7	3.6	—	3.6	15.4	--	1.0	4.0	—
0.7	15.2	—				1.6	23.1	—	2.4	32.0	—
17.3	81.8	12.1									
2.1	24.2	—									
									0.2	4.0	—
14.0	57.6	15.2				2.0	3.8	3.8	15.2	52.0	12.0
0.5	9.1	—	< 0.1	3.6	—						
17.7	66.7	18.3	0.2	3.6	—				19.4	32.0	24.0
100.0		100.0	100.0		100.0	100.0		100.0	100.0		100.0

Table 11. Continued.

Number of fish examined	1954 cont. July 50			1954 August 21			1954 September 35		
	V	F	D	V	F	D	V	F	D
Frogs									
Fish	1.6	2.0	2.0						
Spawn									
Phyllopoda, plankt.	0.1	2.0	—	2.4	4.8	—			
Eurycercus	2.4	4.0					4.3	8.6	5.7
Gammarus	4.9	18.0	6.0	6.0	23.8	4.8	0.4	5.7	—
Asellus									
Limnaea	1.2	8.0	—	4.8	14.3	9.5			
Planorbis	4.8	16.0	6.0	15.0	28.6	14.3	3.4	5.7	2.9
Pisidae	0.1	2.0	—						
Oligochaeta									
Hydracarina									
Trichoptera l.	6.9	28.0	6.0	26.0	52.4	28.5	2.6	2.9	2.9
Ephemeroptera l. ..	15.2	24.0	18.1	6.9	9.5	4.8			
Plecoptera l.									
Megaloptera l.				0.1	4.8	—			
Coleoptera l. (aq.) .	0.3	4.0	—	3.2	28.6	—			
Chironomidae l. ..	0.2	6.0	—						
Simuliidae l.									
Tipulidae l.	1.7	6.0	—	13.1	19.0	19.0			
Coleoptera i. (aq.) .				1.4	4.8	—			
Trichoptera p. i. ..	5.0	16.0	2.0	7.4	14.3	4.8			
Ephemeroptera i. ..									
Plecoptera i.									
Megaloptera i.				0.1	4.8	—			
Chironomidae p. i. .	6.8	16.0	2.0	3.1	9.5	4.8			
Tipulidae i.	2.0	6.0	2.0	0.7	4.8	—			
Terr. *insecta*	46.8	68.0	52.0	9.8	14.3	9.5	89.3	94.3	88.5
Miscellaneous									
Percentage sum ...	100.0		100.0	100.0		100.0	100.0		100.0

| 1954 October | | | 1954 Nov.—Dec. | | |
| 5 | | | 7 | | |
V	F	D	V	F	D
			14.3	14.3	14.3
20.0	20.0	20.0			
25.0	40.0	40.0	5.7	14.3	—
3.0	20.0	—			
32.0	60.0	20.0	65.7	71.4	71.4
			14.3	14.3	14.3
20.0	20.0	20.0			
100.0		100.0	100.0		100.0

Table 12. Food of char. Lake Blåsjön 1944—1954.

(Abbreviations, see table 11!)

Number of fish examined	1944 July 32			1945 August 25			1945 Sept.—Oct. 21	
	V	F	D	V	F	D	F	D
Fish								
Spawn							4.8	4.8
Copepoda	0.1	3.4	—	32.3	36.0	32.0	9.5	9.5
Phyllopoda, plankt.	24.7	44.8	24.2	27.7	40.0	28.0	38.1	23.8
Eurycercus	5.2	13.8	6.9	23.7	28.0	24.0	85.7	57.1
Lepidurus				4.0	4.0	4.0		
Gammarus	7.8	17.2	10.4	6.2	12.0	8.0	4.8	—
Limnaea	17.8	31.0	13.9	4.0	4.0	4.0	4.8	—
Planorbis	3.4	10.3	3.4				4.8	---
Pisidae	0.4	13.8	—	2.0	8.0	—		
Oligochaeta								
Hydracarina	< 0.1	6.9	—					
Trichoptera l.	3.9	17.2	3.4					
Ephemeroptera l...	2.8	17.2	3.4					
Plecoptera l.								
Megaloptera l.								
Coleoptera l. (aq.) .	< 0.1	3.4	—					
Chironomidae l. ..	0.2	24.1	—	0.1	12.0	---	4.8	—
Simuliidae l.	< 0.1	6.9	---					
Tipulidae l.								
Coleoptera i. (aq.) .								
Trichoptera p. i. ..	0.8	6.9	—					
Ephemeroptera i...								
Plecoptera i.								
Megaloptera i.	0.3	3.4						
Chironomidae p. i..	11.9	44.8	10.3	0.1	8.0	—		
Tipulidae i.	13.4	34.5	13.8					
Terr. insecta	7.4	31.0	10.3				9.5	4.8
Miscellaneous								
Percentage sum ...	100.0		100.0	100.0		100.0		100.0

1946 May—June 16			1946 July 44			1946 Augusti 38			1946 September 90		
V	F	D	V	F	D	V	F	D	V	F	D
0.6	6.3	---							4.2	4.4	4.4
			3.2	6.8	2.3	11.2	28.9	15.8	14.9	20.0	15.6
1.8	12.5	-—	10.0	22.7	11.6	14.1	36.8	13.6	31.5	42.2	32.2
3.6	18.8	—	20.4	38.6	20.9	1.5	15.8	2.6	31.7	51.1	34.4
			12.9	22.7	14.0	14.2	42.1	10.5	3.8	15.6	3.3
			0.7	4.5	—	0.4	5.3	—	< 0.1	1.1	—
1.7	6.3	—	0.4	11.4	—	< 0.1	2.6	—	2.7	24.4	2.1
			0.2	2.3	—						
			0.2	15.9	—	< 0.1	7.9	—	0.1	2.2	—
			1.4	20.5	2.3	9.5	26.3	7.9	2.0	16.7	1.1
2.7	6.3	—	5.5	27.3	4.7	10.7	44.7	10.5			
86.5	93.8	100.0	3.9	34.1	2.3	0.4	10.5	—	1.2	7.7	1.0
			0.1	6.8	—				< 0.1	2.2	—
3.1	18.8	—	2.8	56.8	2.3	7.7	55.3	5.3	0.2	7.7	1.9
			3.6	25.0	—						
						0.7	2.6	—			
			7.3	29.5	9.3	2.9	21.1	2.5	1.2	1.1	1.0
									1.1	1.1	—
									< 0.1	1.1	—
			23.6	61.4	30.3	20.2	60.5	26.3	1.5	7.7	1.0
			1.3	11.4	—	2.6	13.6	2.5	1.4	2.2	1.0
			2.5	43.2	—	3.6	42.1	2.5	2.4	16.7	1.0
						0.3	2.6	—	0.1	2.2	—
100.0		100.0	100.0		100.0	100.0		100.0	100.0		100.0

Table 12. Continued.

Number of fish examined	1946 October 103			1949 June 38			1949 July 50		
	V	F	D	V	F	D	V	F	D
Fish				2.7	2.6	2.7			
Spawn	8.6	9.7	8.7						
Copepoda	< 0.1	1.9	—	1.5	7.9	—	0.1	12.0	—
Phyllopoda, plankt.	52.7	69.9	57.4				67.3	88.0	72.0
Eurycercus	10.9	19.4	6.8						
Lepidurus									
Gammarus	19.2	36.9	23.3	32.4	57.9	38.9	2.3	10.0	2.0
Limnaea	4.1	13.6	1.9	0.1	39.5	—	3.5	8.0	4.0
Planorbis	< 0.1	1.0	—						
Pisidae	0.8	5.8	—	0.2	10.5	—	1.9	6.0	2.0
Oligochaeta									
Hydracarina	< 0.1	1.0	—	< 0.1	5.3	—	< 0.1	2.0	—
Trichoptera l.	< 0.1	2.9	—	5.5	21.0	5.6	3.8	4.0	4.0
Ephemeroptera l. ..				1.2	39.5	—			
Plecoptera l.	0.1	1.0	—	2.9	10.5	2.8			
Megaloptera l.									
Coleoptera l. (aq.) .	< 0.1	1.0	—	0.1	23.7	—			
Chironomidae l. ...	0.5	2.9	—	2.2	65.8	—	7.9	86.0	2.0
Simuliidae l.				< 0.1	39.5	—	< 0.1	8.0	—
Tipulidae l.				< 0.1	2.6	—			
Coleoptera i. (aq.) .									
Trichoptera p. i. ..							< 0.1	2.0	—
Ephemeroptera i...									
Plecoptera i.				< 0.1	2.6	—			
Megaloptera i.									
Chironomidae p. i..	1.0	8.7	—	35.1	76.3	36.1	8.9	30.0	10.0
Tipulidae i.	0.1	1.0	—	< 0.1	5.3	—			
Terr. *insecta*	2.0	2.9	1.9	15.4	57.9	13.9	4.3	18.0	4.0
Miscellaneous									
Percentage sum ...	100.0		100.0	100.0		100.0	100.0		100.0

1949 August 37			1949 September 44			1949 October 29			1954 April—May 43		
V	F	D	V	F	D	V	F	D	V	F	D
						9.5	20.7	13.8			
5.0	8.1	8.1	14.8	25.0	15.9	2.7	6.9	—	4.5	7.0	7.0
59.1	83.8	54.0	62.9	88.6	63.7	71.5	79.3	72.5	2.3	2.3	2.3
23.2	37.8	29.7	5.4	18.2	6.8	8.6	31.0	6.9			
3.3	18.9	2.7	3.8	13.6	2.3	4.6	20.7	3.4	33.1	48.8	34.9
0.3	10.8	—	1.6	9.1	—	0.1	10.3	—	0.2	2.3	—
0.1	2.7	—	< 0.1	2.3	—	< 0.1	3.4	—			
2.8	18.9	2.7	0.2	6.8	—	0.1	13.8	—	0.6	4.7	—
< 0.1	2.7	—							0.1	2.3	—
1.1	5.4	—	0.1	6.8	—				6.1	9.3	7.0
0.2	8.1	—	0.1	4.5	—	< 0.1	3.4	—	8.3	11.6	9.3
									23.0	39.5	18.6
0.4	40.5	—	< 0.1	4.5	—	2.8	44.8	3.4	14.4	32.6	11.6
									1.4	2.3	2.3
			0.5	13.6	—						
			0.1	2.3	—						
									0.2	2.3	—
						0.1	6.9	—	0.2	2.3	—
4.4	45.9	2.7	5.1	52.3	6.8	0.1	< 3.4	—	1.9	4.7	2.3
			0.6	11.4	—						
0.1	13.5	—	4.6	27.3	4.5	< 0.1	3.4	—	1.4	2.3	2.3
									2.3	2.3	2.3
100.0		100.0	100.0		100.0	100.0		100.0	100.0		100.0

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Table 12. Continued.

Number of fish examined	1954 June 46			1954 July 38			1954 August 41		
	V	F	D	V	F	D	V	F	D
Fish							2.0	2.4	2.4
Spawn									
Copepoda	0.1	4.3	—	24.4	26.3	23.7	16.0	17.1	17.1
Phyllopoda, plankt.	27.7	43.5	34.8	30.3	42.1	31.6	23.8	36.6	24.4
Eurycercus				12.5	15.8	13.2	30.3	41.5	31.8
Lepidurus									
Gammarus	4.3	8.9	4.3	2.2	7.9	5.3	1.2	4.9	—
Limnaea	1.4	4.3	2.2	2.7	2.6	2.6			
Planorbis				0.4	2.6	—			
Pisidae	1.0	6.5	—	2.6	2.6	2.6	< 0.1	4.9	—
Oligochaeta	1.2	6.5	—						
Hydracarina									
Trichoptera l.	0.2	2.2	—	0.9	2.6	—			
Ephemeroptera l. .	0.2	2.2	—	2.1	5.3	2.6	5.5	12.2	4.9
Plecoptera l.									
Megaloptera l.									
Coleoptera l. (aq.) .	0.4	2.2	—				0.1	4.9	—
Chironomidae l. ..	2.9	47.8	2.2	2.2	13.2	2.6	14.0	31.7	14.6
Simuliidae l.	0.7	17.4	—						
Tipulidae l.	0.2	2.2	—						
Coleoptera i. (aq.) .	< 0.1	4.3	—						
Trichoptera p. i. ..							2.2	2.4	2.4
Ephemeroptera i. ..									
Plecoptera i.				0.3	5.3	—			
Megaloptera i.				0.1	2.6	—			
Chironomidae p. i. .	50.5	89.1	52.2	9.5	47.2	7.9	4.4	26.8	2.4
Tipulidae i.	2.4	15.2	—	2.6	15.8	—			
Terr. insecta	6.9	26.1	4.3	7.2	28.9	7.9	0.5	7.3	—
Miscellaneous									
Percentage sum ...	100.0		100.0	100.0		100.0	100.0		100.0

1954 September 38			1954 October 25			1954 Nov.—Dec. 12		
V	F	D	V	F	D	V	F	D
			19.4	24.0	16.0			
13.3	18.4	13.1	4.4	8.0	8.0	0.4	8.3	—
16.0	21.1	15.8	56.6	72.0	60.0	1.7	8.3	—
21.2	26.3	23.7	7.4	20.0	12.0			
0.7	2.6	—	1.8	4.0	—	20.0	50.0	16.7
			2.0	4.0	4.0			
0.1	2.6	—	4.6	16.0	—			
						7.9	16.7	8.3
						2.5	8.3	—
						17.5	41.7	16.7
						3.3	41.7	16.7
						46.7	75.0	50.0
			0.4	4.0	—			
48.7	57.9	47.4	3.4	8.0	—			
100.0		100.0	100.0		100.0	100.0		100.0

Table 13. Food of char. Lake Korsvattnet 1943—1947. (Abbreviations, see table 11!) Figures obtained by means of the volumetrical method (V).

	1943 July	1944 July »Great»	1944 Sept. »Great»	1944 July »Dwarf»	1944 Sept. »Dwarf»	1945 July	1945 Sept.	1947 July
Number of fish examined	30	17	10	21	24	31	8	44
Fish	5.0	3.5	16.0				78.8	4.5
Spawn					4.2		21.2	
Phyllopoda, plankt.				47.1	9.6	0.9		13.1
Eurycercus	7.3	21.2		24.4	23.3	8.1		
Limnaea	2.7		7.0		2.9	0.3		
Pisidae					1.5			
Trichoptera l.		3.5	10.0	4.6		3.2		1.0
Ephemeroptera l.	0.5							
Plecoptera l.	1.0				0.2	0.6		
Coleoptera l. (aq.)				0.7		0.3		
Chironomidae l.	4.2	3.5		2.1	32.5	8.4		6.3
Simuliidae l.				7.5				
Tipulidae l.	0.5			0.4	1.5	0.3		
Coleoptera i.	0.7			1.1	0.6			
Trichoptera p. i.	5.3	3.5	44.0	2.1	4.2	8.1		0.5
Ephemeroptera i.				5.0				
Plecoptera i.	6.0	1.8		0.7				0.5
Chironomidae p. i.	25.3	54.7		1.8	5.8	51.6		9.9
Tipulidae i.	4.5			0.7			11.3	29.4
Terr. *insecta*	35.0	8.2	23.0	1.4	4.8	6.9		34.8
Miscellaneous	2.0							
Percentage sum	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Table 14. Mean temperature at Gäddede (from Sveriges Meteorologiska och Hydrologiska Institut, Årsbok) and the surface water of Lake Blåsjön. (0.1 m).

	April	May	June	July	August	Sept.	October
1944 (air)	— 1.4	3.3	8.6	13.9	11.9	7.8	4.6
1945 (air)	1.3	5.4	10.9	15.1	13.7	6.7	1.7
1946 (air)	1.5	5.7	9.6	14.0	12.4	9.5	3.6
1946 (water)		1.0	—	16.0	13.0		
1948 (air)	2.9	6.5	10.3	14.8	10.0	7.8	1.9
1949 (air)	0.5	6.3	10.4	11.7	10.6	10.6	3.5
1949 (water)			6.0	9.5	10.0		
1953 (air)	1.4	5.2	14.5	12.9	12.7	7.1	4.8
1954 (air)	— 0.4	8.3	9.8	14.0	11.8	7.1	1.7
1901—1930 normal (air) ..	— 0.3	4.4	9.1	12.6	11.2	7.0	1.9

Table 15. Average weight and length of fish feeding on certain food objects (=dominating food item) in Lake Blåsjön 1954. w=weight, l=length.

	Char						Trout					
	May—June Aver.		July—Aug. Aver.		Sept.—Oct. Aver.		May—June Aver.		July—Aug. Aver.		Sept.—Oct. Aver.	
	w.	l.	w.	l.	w.	l.	w.	l.	w.	l.	w.	l.
Average weight	205		283		225		354		149		189	
Average length		274		302		273		305		241		262
Frogs							2,650	600				
Fish			250	320			500	400	350	340		
Spawn					230	290					350	350
Copepoda	192	277	272	303	211	268						
Phyllopoda	229	286	234	287	128	228						
Eurycercus			296	297	277	301						
Gammarus	175	251	610	390			363	332	220	240	270	305
Limnaea	350	340	600	405	225	275			293	250		
Planorbis									198	267	230	275
Pisidae			575	385								
Trichoptera l.	257	283					271	303	199	275	173	256
Ephemeropt. l.	218	275	367	323					114	225		
Plecoptera l.	171	251					305	325				
Coleoptera l.							275	305				
Chironomidae l.	145	245	324	330			90	208				
Tipulidae l.	215	290							263	296		
Trichoptera p. i.			230	265					145	253		
Chironomidae p. i. ..	226	295	175	270			211	253	140	235		
Tipulidae i.									110	220		
Terr. insecta	233	290	300	320	239	274	200	260	101	218	182	257

Salmon Stock Fluctuations in the Baltic Sea

By Gunnar Svärdson

Introduction

The salmon (*Salmo salar* L.) is one of the most important species of fish in the Baltic Sea from a commercial point of view. Unlike other populations of the atlantic salmon that of the Baltic is heavily fished during its period of pelagic sea life. Like the other populations, however, it is also fished when the adult specimens after some years of feeding and rapid growth return to their home river to spawn. The baltic salmon is, therefore, fished as a comparatively small fish in the sea, and as a considerably larger fish later on, in the rivers or the estuaries.

The first student of salmon in Sweden, GISLER (1752), reported that every year hooks, often with a few feet of line still attached, were found on salmon ascending the River Ångermanälven. Two strange hooks were found on salmon in 1728 and hooks were reported to him in 1746 from the still more northerly River Lule. GISLER brought some of the hooks to the Academy of Science in Stockholm and experts found that the hooks were of a type used for cod in Gotland, Öland or on the coast of the Swedish Province of Bleking in the southern Baltic.

NILSSON (1855) stated that salmon hooks originating from the Pomeranian coast of Germany had been found in northern Sweden. LILJEBORG (1891) added that Finnish salmon had born hooks from Rügen and Memel. Gradually the finds accumulated and formed a considerable body of evidence indicating long salmon migrations within the Baltic. The evidence obtained was summarized by QUEDNAU (1932), who used the method with previously marked hooks to obtain more facts about the salmon migrations.

When ROSÉN (1918 a, 1918 b) had confirmed for the Baltic DAHL's (1910) discovery of the high smolt age in northern salmon and ALM (1919) reported a much lower smolt age for the salmon in the River Mörrumsån in the southern Baltic, a new possibility arose for proving the distant migrations in the sea. HESSLE (1923 a) reported a dominantly high smolt age from the scales of salmon caught in the sea off the Isle of Gotland, DIXON (1931) found most of the salmon caught off the Polish coast to be of northern origin and the

same was reported by WILLER and QUEDNAU (1931) for the East Prussian coast. This method of scale-reading thus proved once again the distant migrations and the fact that most of the salmon caught in the central and southern Baltic originated in the rivers far north.

The tagging schemes of the Baltic countries have given still further evidence, again confirming the principal movements. The first results (TRYBOM 1908 a, 1910, 1911) have been followed by hundreds, and, more recently, thousands of recovered tagged salmon. Only part of this bulky material has so far been published in scattered reports (ALM 1934, CARLIN 1955). A new and comprehensive international summary of all the salmon recoveries in the Baltic is much needed for reference and detailed study.

The smolts from northern Swedish rivers move south along the coast, following the dominating current of the sea, moving counterclockwise round the south basin of the Baltic Sea. Whether the Finnish smolts first move across the Gulf of Bothnia to the Swedish coast until they move south is not quite clear, nor are the movements of the German and Baltic salmon smolts. Some of the tagged smolts from German, Polish and Latvian rivers were found during their first or second summers along the Swedish coast in the Gulf of Bothnia. They may very well have been driven north by the dominant current off the eastern shore of the sea.

The fluctuations of the Baltic stock of salmon are a matter of interest to all nations bordering on the Baltic Sea. In recent years the future of the Baltic salmon has been seriously menaced by the increasing utilization of the great northern rivers for hydroelectric purposes. Turbines, dams and small lakes replace the rapids, where the salmon used to spawn and their fry was hatched.

Hypotheses about Salmon Stock Fluctuations

The records of catches from the sea are inferior to the river records as a gauge for the fluctuations in the Baltic salmon stock. Firstly sea fishery is much more influenced by war conditions, such as have arisen twice in this century. Secondly sea fishery lags behind the fluctuations in the stock. When salmon increased in 1919—1920 a sea fishery gradually developed off Gotland (HESSLE 1923 a) and the recent increase of the Baltic stock was followed by increased efficiency in sea fishery (ROSÉN 1949, LINDROTH 1950, ALM 1954).

The principal catches of salmon in the estuaries or the rivers in northern Sweden and Finland are made by seines and a special form of salmon weir or trap. These are described by ROSÉN (1918 a) and JÄRVI (1938). Some of them are selective in relation to the water level and they catch fewer salmon at low water (OLOFSSON 1935), when the fish are said to go farther from land outside the effective part of the trap.

In spite of the pitfalls in the statistics it has been known for a long time

that there were pronounced parallel trends in the output of the salmon fishe-
ries in adjoining rivers (LING 1901) or over larger areas (TRYBOM 1908 a,
HENKING 1916, ALM 1924). Moreover, some slight tendency towards still more
parallel trends in salmon fishery were pointed out by ALM (1928), when he
found the decrease during the 1890's (see below) had also occurred in the
Netherlands. Some similarities were also found in the fishery of Great Britain
and Norway.

Apart from smaller fluctuations, the most prominent trend for the salmon
stock in the Baltic Sea was the catastrophic fall in yields during the 1890's,
when in only ten years the catch was reduced to a mere fraction (LING 1901).
This fact was the basis for all the hypotheses about the biological causes put
forward by the salmon experts in the Baltic Section of the International Com-
mittee of Sea Exploration (see TRYBOM and HENKING). Climate, predators,
new timber-logging practices, variations in water level etc. were discussed but
no means for reversing the trend were recommended other than extensive
plantings of salmon fry.

Two major lines of thought later crystallized. Both considered that the
year classes became reduced at an early stage, in fresh water during the very
first winter of salmon development. ALM (1924) and HAGMAN (1938) looked
upon the variations in water level as being the most potent factor for creating
good or bad year classes but JÄRVI (1938, 1947, 1948) found that the water
level was only of secondary importance, the most important thing being,
according to this author, the number of spawning salmon parents. JÄRVI
thought he could find a regular recurrence of rich year classes, seven years
apart. This corresponds to a cyclical fall in salmon yield on the American
side of the Atlantic (HUNTSMAN 1938, 1941) and, in some respects, to the
cyclical dominance in sockeye salmon described by RICKER (1950).

The sudden rise of the Baltic salmon population in the 1940's to a level not
seen for 50 years set both these hypotheses aside. No major change in water
level in the rivers had occurred and, further more, the series of rich new
year classes was born to parents, which had been extremely scarce. LINDROTH
(1950) made a most valuable survey of the possibilities that remained. The
remarkable coincidence of the record winters of 1940—1942, the coldest
sequence for three winters ever recorded (LILJEQUIST 1943), had been dis-
cussed by Swedish fishery biologists interested in the problem of *salmon
redivivus*. LINDROTH tried to make a statistical correlation between salmon
catches and winter temperatures, but the coefficient was insignificant. Data
on the ice conditions of the Baltic were suggestive but not sufficiently de-
tailed for an exact comparison. LINDROTH confined himself to the conclusion
that the abundance of salmon was due to the biological balance between sal-
mon and some other species.

Ice Covering of the Baltic Sea and the Salmon Yield

In a symposium about the recent change in climate in Scandinavia, JURVA (1952) published data over the ice conditions of the Baltic for 120 years. It is, therefore, now possible to extend the study on the relations between ice and salmon yield, started by LINDROTH (1950) with more scanty material.

According to JURVA, the probability for freezing varies very much in different parts of the Baltic. North of a line Stockholm—Tallinn (Reval) the probability for freezing is greater than 50 per cent. The sounds between the Danish islands and southern Sweden are frozen every third winter, but the waters round the Isle of Bornholm are frozen only in one winter out of every five (probability 20 per cent). The central region of the south Baltic, off Gotland, has a probability for freezing of only 5 per cent.

Ice increases gradually during the winter in the Baltic, having its maximum covering in March. The largest possible area of ice, the whole sea, is 420,000 square kilometres. The period of 120 years contains nine winters of exceptional intensity and severe ice conditions with the whole sea covered. These

Table 1. Area of maximum ice in the Baltic 1830—1951, adapted from JURVA (1952). (Unit ice area = 10,000 square kilometres.)

| Year	Area	Year	Area	Year	Area	Year	Area
1830	42	1861	32	1892	25	1922	26
31	33	62	34	93	42	23	33
32	10	63	9	94	8	24	28
33	9	64	8	95	28	25	9
34	23	65	36	96	14	26	38
35	7	66	10	97	18	27	12
36	39	67	42	98	14	28	18
37	17	68	41	99	18	29	39
38	41	69	13	1900	33	30	6
39	32	70	18	01	18	31	17
40	36	71	42	02	36	32	15
41	37	72	12	03	9	33	15
42	8	73	9	04	17	34	11
43	9	74	9	05	13	35	9
44	38	75	33	06	9	36	15
45	39	76	41	07	14	37	16
46	18	77	42	08	23	38	7
47	28	78	8	09	18	39	6
48	13	79	14	10	8	40	42
49	18	80	13	11	11	41	39
50	33	81	42	12	16	42	42
51	18	82	8	13	12	43	9
52	17	83	34	14	13	44	6
53	31	84	12	15	18	45	11
54	13	85	16	16	33	46	21
55	31	86	20	17	40	47	41
56	41	87	9	18	16	48	20
57	22	88	42	19	15	49	7
58	9	89	33	20	15	50	11
59	8	90	8	21	13	51	15
60	18	91	12				

230
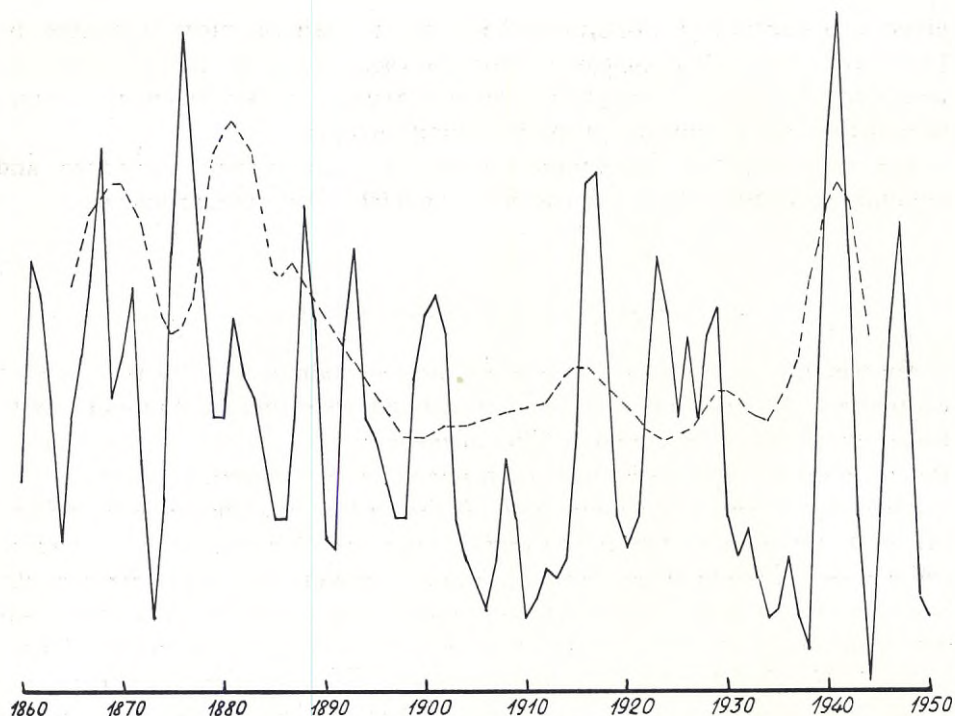
Fig. 1. Smoothed trend of maximum ice cover in the Baltic (solid line) during the period 1860—1950, according to Jurva (1952). Smoothed trend of salmon yield in Swedish rivers (broken line) according to Lindroth (1950). The salmon catch is put back five years, relatively to the ice data.

nine winters were, ranked according to the severity of their ice conditions: 1871, 1877, 1940, 1893, 1942, 1881, 1888, 1867, and 1830. In the present paper, as in Jurva's, all the winters are denoted by one year only, that of the »spring» part of the winter, i.e. January—March.

It is interesting to note that after 1830 the Baltic was never totally frozen until 1867, a period of nearly 40 years. This first »warm» period was followed by the colder one in the 70's, 80's and early 90's, when the whole sea was frozen five times. After 1893 the sea was never again wholly covered in ice until 1940, followed by the new record winter of 1942, the intermediate winter, 1941, being only slightly milder. Roughly speaking there was an early warm period of 40 years, then a cold one of 30 years and finally a warm period again of 50 years, terminating abruptly in the 1940's. The details of the winters, reduced to an »index» of ice cover, are condensed in Table 1. In the table the »index» 30 means 30 times the unit of 10,000 square kilometres of ice.

To illustrate the general trend of change in climate, Jurva has levelled the index of ice covering in averages for three consecutive years and this curve is

given here as Figure 1, drawn together with the »salmon curve» presented by LINDROTH (1950). It is suggestive that the two curves run parallel. The salmon curve has been put back five years in relation to the ice curve, for reasons which will be obvious in the following sections.

The coefficient of correlation for the two curves was calculated and amounts to 0.3405, which corresponds to a 0.002 level of significance.

Peak Years of Salmon Yield

Another line of study on the relation between salmon and ice is a detailed comparison of different peak years of salmon yield and various notes published about salmon abundance. The primary data about the salmon yield in the different Swedish rivers have been published by LINDROTH (1950).

1898 was a peak year, giving a small rise in the otherwise constantly falling curve for salmon yield in the 1890's. That year there was a peak catch in the Rivers Ångermanälven, Indalsälven and Ljungan. The year 1896 was the best year in the Rivers Ume and Mörrumsån and finally the year 1897 was the peak one in the River Dalälven. Data are lacking for the Rivers Torne, Kalix, Lule, Skellefte, Ljusnan and Klarälven. The last mentioned runs into Lake Vänern, where the salmon is landlocked and cannot move out to the sea. Its growth and movements were discussed by RUNNSTRÖM (1940) and TÖRNQUIST (1940).

In the sea fishery at Bornholm there was a peak in 1896 (TRYBOM 1910).

The winter of 1893 was the last one for a long time during which the Baltic Sea was totally frozen (Table 1). The lapse of time to the salmon peak was 3—5 years.

1905 and *1908*. Though the output of the salmon fishery was generally low, there were some small peaks in these two years. In 1905 a peak occurred in the Rivers Torne, Kalix, Ångermanälven, Indalsälven and Ljungan, in 1906 in the River Klarälven, in 1907 in the River Mörrumsån and in 1908 yet another peak in the Rivers Torne, Kalix, Ume, Indalsälven and Dalälven.

There was a severe winter in 1900 (index 33) and again in 1902 (index 36).

1921. The increase about 1921 has been noted and discussed by ALM (1934). There was a peak in 1920 in the Rivers Mörrumsån and Klarälven, in 1921 the Rivers Torne, Lule, Ångermanälven and Ljungan culminated. Some did not reach a peak until 1923, notably the Rivers Ume, Indalsälven, Ljungan, Ljusnan and Dalälven.

The two winters of 1916 and 1917 had a considerable ice covering (indexes 33 and 40).

1927. Peak salmon yields in this year were reported from the Rivers Ume, Ljungan, Ljusnan and Dalälven and a rather slight peak from the River Mörrumsån. In LINDROTH's tables data are lacking for the Rivers Torne, Kalix

and Lule but from OLOFSSON (1942) it can be seen that the Province of Norrbotten had a peak that year, including the River Lule. It is also interesting that an exceptional abundance of small salmon was noted by OLOFSSON in 1925 in the Gulf of Bothnia (OLOFSSON, 1926) and the same happened on the Finnish side of the Gulf (JÄRVI 1938). OLOFSSON noted from the scales that the abundant small salmon did not belong to one year class and that they had been in the sea for one (grilse) or two years, some displaying poor growth.

There was a severe winter in 1923 (index 33).

1934. This was a peak year for the Rivers Torne, Kalix, Skellefte, Ume, Indalsälven, Ljungan and Ljusnan. Some culminated in 1933 such as the River Dalälven, and also the Ljungan (second peak) but others not until 1935, as did the Rivers Mörrumsån, Klarälven and Ljusnan (second peak). The rise of the River Ångermanälven in 1934 was followed by a further increase, culminating in 1936.

In 1930 the number of small salmon in the northern Baltic increased (ALM 1931) but not until the summer of 1931 was the number of grilse really great (OLOFSSON 1932, JÄRVI 1938). OLOFSSON again found one or two years of sea life and some fish with poor growth. In the winter of 1931 and December 1930 small salmon with one or two years of sea life were exceptionally abundant off the German coast (WILLER and QUEDNAU 1934).

There was a severe winter in 1929, the index for which rose to 39.

1945—1947. The rise of the salmon population in the Baltic culminated in these years. The peak was in 1945 in the Rivers Kalix, Ångermanälven and Indalsälven. It was noted in the year 1946 for the Rivers Torne, Lule, Ljungan, Ljusnan and finally in 1947 for the Rivers Ume, Ljungan and Klarälven.

The three record winters discussed were 1940—1942. The lapse was the usual five years.

1952. The decline, continuing since the very peak in the 1940's, was temporarily stopped by a small rise in 1952. This peak was noted in the Rivers Kalix, Lule, Skellefte, Ume and Ångermanälven.

There was a severe winter in 1947, the index for which was very high, 41. The time lapse was five years.

This survey has shown that there is a remarkable tendency for the Swedish rivers to react with the same trend to some factors, which might have something to do with severe winters. It becomes still more probable that climate is in some way responsible for this trend, when it is found that the same similarity of trend is found elsewhere.

HUTTON (1930 a) demonstrated that six British salmon rivers fluctuated in the same way, displaying peaks in the very same year. There was a peak in the River Wye in 1913, in Norway in 1914 (HUTTON 1930 b) and in the Southern Baltic in 1913 (WILLER and QUEDNAU 1931).

The Swedish peak in 1921 was contemporary to a Norwegian peak salmon yield the same year, as can be seen in the graph published by HUTTON (1930 b) and SØMME (1948).

WENT (1939) pointed out that in 1927 there had been a peak in salmon yield in England, Scotland and Ireland. From HUTTON (1930 b) and SØMME (1948) it can be seen that Norway also had a peak in 1926—1927, STEINERT (1931) reported a peak in the Rhine and Maas in 1927 and it has been reported above that 1927 was a peak year in all northern Swedish rivers as well. SIEDLECKI (1932, 1936) noted the similarity of salmon abundance in 1927 in different countries and found it most probably indicated rich year classes in all areas.

The peak abundance of grilse in 1931 in the northern Baltic just mentioned above had a parallel in southern Norway (DANNEVIG 1949) and HUTTON reported (1932) an increase in the number of grilse, observed in 1931, over the whole of England.

Finally, the peak 1934—1935 in the Baltic is contemporary to the peak 1935—1936 in England, Scotland and Ireland (WENT 1939) and the start of the peak period 1935—1939 in Norway (SØMME 1948).

HUTTON has suggested in a series of papers on the salmon of the River Wye, that some fundamental factor regulating the fluctuations was at work in the sea. He suggested the influence of the Gulf Stream, and this could mean a variation in the water temperature in different summers.

With regard to the Baltic it must, however, be pointed out that the fluctuations are of greater or lesser extent. The great periodic decline and rise in the salmon population is not paralleled elsewhere, at least not the recent dramatic rise in the population. The factor mainly influencing the salmon population of the Baltic might, therefore, be of a kind not found outside it, though some other less active factors are common to larger areas. The fact that the trend is not parallel in every year between such distant areas as the Baltic, Norway or the British Isles suggests climate as being responsible, since only in a few years is the summer very warm or the winter exceptionally cold over such large areas. It depends on general meteorological conditions and the position of more or less stable regions of high and low pressure.

Statistics from the Svartö Weir in the River Lule for 150 years

Situated at the mouth of the River Lule is the Svartö Weir, famous for its unbroken series of statistics from 1804. Catch figures for the years 1804—1921 were published by ALM (1924) and thanks to the kindness of Mr. ERIK MATTSON, Luleå, I have had access to figures for the years 1922—1953. All data are collected in Table 2.

The Svartö Weir is known to fish selectively depending on the water level

Table 2. Salmon yield in deci-tons, Svartö Weir at the mouth of the River Lule, during the years 1804—1953.

Year	Deci-tons	Year	Deci-tons	Year	Deci-tons	Year	Deci-tons	Year	Deci-tons
1804	96	1834	141	1864	60	1894	67	1924	16
05	76	35	239	65	60	95	45	25	5
06	84	36	195	66	75	96	77	26	3
07	117	37	45	67	15	97	37	27	41
08	200	38	75	68	60	98	46	28	21
09	187	39	15	69	52	99	30	29	7
10	126	40	34	70	30	1900	30	30	24
11	164	41	94	71	75	01	13	31	7
12	106	42	109	72	45	02	8	32	28
13	67	43	239	73	57	03	9	33	13
14	88	44	123	74	218	04	15	34	13
15	43	45	105	75	152	05	17	35	54
16	70	46	37	76	288	06	13	36	10
17	165	47	123	77	161	07	6	37	4
18	98	48	33	78	87	08	6	38	21
19	130	49	111	79	19	09	8	39	13
20	106	50	49	80	92	10	9	40	—
21	148	51	90	81	122	11	5	41	13
22	193	52	75	82	129	12	—	42	20
23	184	53	52	83	39	13	7	43	24
24	171	54	150	84	240	14	16	44	23
25	118	55	30	85	238	15	18	45	38
26	569	56	195	86	133	16	7	46	51
27	260	57	86	87	124	17	27	47	31
28	142	58	90	88	37	18	12	48	20
29	103	59	90	89	24	19	20	49	20
30	157	60	142	90	111	20	41	50	22
31	76	61	299	91	62	21	29	51	12
32	135	62	135	92	72	22	3	52	34
33	88	63	105	93	100	23	17	53	5

(OLOFSSON 1935). The record yield in 1934 was thus not registered in the weir owing to low water. On the whole, however, it probably can be regarded as being representative for the River Lule and the whole of the northern Baltic.

The first peak registered at Svartö was 1808—1809. Ice data are not available until 1830 but the temperature data published by LILJEQUIST (1943) disclose that the three winters 1803—1805 were all very cold. The mean temperature December—March was −5.1°, −6.0° and −6.0° C for the three years, a figure much lower than the average for the decade (−4.1°). In 1931—1940 the mean temperature was −1.2° C.

The cold winter of 1814 (mean temperature December—March −6.8° C) was followed by a period of high yield at Svartö, starting in 1819. The cold winter of 1821, followed by a record mild winter (mean temperature resp. −3.6° C and +2.0° C), brought about the absolute record catch at Svartö in 1826. The lapse of five years is the usual one. The combination of a cold winter, followed immediately by a mild one is also met with in 1929—1930, bringing about the salmon peak in 1934 (see above).

Table 3. Average salmon catch in deci-tons at the Svartö Weir at varying intervals after winters with different ice conditions.

If the winter is put at zero, the catch has been made during the year	Group 1 46 mild winters less than 150,000 km² of ice	Group 2 34 average winters 150—290,000 km² of ice	Group 3 38 severe winters more than 290,000 km² of Baltic ice	P 1	P 2
1	64.5	56.0	78.1	> 0.05	> 0.05
2	82.7	45.7	65.0	0.04	> 0.05
3	73.6	39.2	76.6	0.03	> 0.05
4	57.2	52.3	83.3	> 0.05	0.04
5	57.0	47.7	85.2	0.04	0.01
6	58.1	46.5	78.8	> 0.05	0.04
4—5	116.5	102.3	168.5	0.03	0.01
5—6	119.7	94.2	164.1	0.04	0.02
4—6	181.3	150.6	247.4	0.04	0.02

P 1 means the probability that chance is responsible for all differences between the three groups.

P 2 means the probability that chance is responsible for the difference between group 3 compared with the two others.

For the period 1830—1950 the yield at Svartö and the ice covering of the Baltic can be compared annually (Tables 1 and 2). For a further analysis, the winters were divided into three groups comprising mild, average and severe winters. The mild winters were 46 in number, all having less than 150,000 square kilometres of ice in the Baltic. The severe winters numbered 38, all having more than 300,000 square kilometres of ice. The rest, 34 in number, were classed as average winters.

For every winter a number of corresponding salmon yields could be studied. By comparing the catch after a lapse of one, two, three or more years after each type of winter, it was possible to go into greater detail regarding the time-relations than previously. The results are given in Table 3. The differences between the three types of winter were analysed as regards the variance according to the methods described in BONNIER and TEDIN (1940).

From Table 3 the following main preliminary conclusions can be drawn:

1. After a mild winter the salmon yield increases, culminating in the third summer after the winter in question.
2. After a severe winter the salmon yield increases significantly, culminating in the sixth summer after the winter in question.
3. An average winter is followed by an average salmon yield for all intervals of up to six years.

Ice Cover in Winter and Spring Warming of the Sea

Since 1923 the temperature has been recorded daily on a few Swedish lightships in the Baltic and the material has been published. From this

source the relations between ice cover in winter and the warming up of the sea in spring can be studied. Some of the most important temperature figures were published by ALM (1934). There is a serious gap in the material during the war and the years immediately following.

The lowest temperature for the Baltic Sea is normally found in March, which is also the month for the most widespread ice. The warming up, however, proceeds rather rapidly and in June the temperature is mainly dependent on the actual meteorological situation, that is to say the temperature of the sea lags behind the temperature of the air but the aftereffect of the severity of winter is overcome.

During April and May, two most important months for the salmon, the temperature of the sea is, however, dependent both on the loss of heat during the previous winter and the actual temperature of the air, the temperature of the sea being a compromise.

From Table 1 can be seen that the winters of 1925 and 1930 were rather free from ice. This corresponds to the temperature of the sea and these two years had outstandingly high temperatures during January. In March they were not the only years to be exceptional in the recorded material as there were some more years with high sea temperature, i.e. 1934 and 1938. In April the record temperature for the Baltic was noted for 1925, 1930, 1934, 1938 and 1950. In the next month, May, 1925, 1930, 1934 and 1950 were warmest, the year 1938 no longer being exceptional but merely normal. Lastly in June, 1930 still stands out as being the record year, 1925 continued to have a high temperature though proportionately lower than the previous month, while 1934 and 1938 were both normal. 1950 was warm only in the northern part of the Baltic and 1943, for which year very few data are available, might, if judged from one single monthly average, also have been very warm and early.

The indexes of ice cover for the winters preceding these warm springs were 9, 6, 11, 7, 9 and 11. All of them were, therefore, classed as mild winters in Table 1.

The coldest months of April and May were, on the other hand, the years 1924, 1929, 1931 and the three consecutive years 1940, 1941 and 1942. For these last three years no Swedish data are available but SALOMONSEN (1943) gives the record low spring temperature for the sea around the Isle of Bornholm. These six coldest springs were recorded after winters with the following ice covering: 28, 39, 17, 42, 39, and 42. An example of a heavy winter followed by a warm spring was 1947. Very few data exist for that year but those that do indicate exceptional cold for the sea in May but normal temperature in June.

The rule that can be inferred from these data is that a heavy winter is most often followed by cold spring months in the sea but a mild winter by a high temperature in spring.
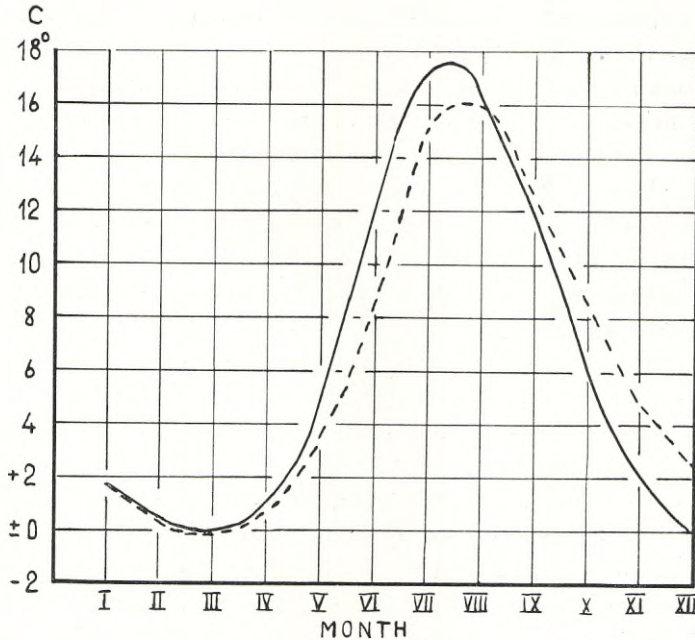
Fig. 2. Temperature during the year in the River Ljusnan at Framnäs (solid line), according to MELIN (1938) and the temperature in the sea at the Isle of Agö (broken line), drawn from some data published by ÖSTMAN (1939).

The Effect of a Warm Spring on Salmon Run

The average temperature curve for the year runs somewhat differently in the river, as compared to the sea (Figure 2). Since the sea is a very large body of water indeed, its power of storing heat makes it always a step behind the river in the annual temperature cycle. In the spring and early summer the river is warmer than the sea, homothermy is reached about August 1st or a few days later and after that the sea is warmer than the river for the remainder of the year. A salmon rising for the run in the river must, therefore, start before August if it is to head into warmer water. After that date, no more runs seem to occur in Swedish rivers. Regarding smolt the argument of course is the opposite; they must head into a colder sea if they descend before August. After that date and during the autumn the smolt can swim into the sea and move south following a trend towards warmer water.

Some scanty data on the temperature of the Baltic, collected for the months May—November only, are available for the years 1880—1913. From these data can be seen that, in the northern Baltic, the years 1886, 1896 and 1905 had warm months of June.

Salmon statistics for 1886 are available only for a few rivers. The year 1886 was by far the best ever recorded for the Ume River. The other two

years have appeared earlier, in the previous sections of this paper, as peak years in some Swedish rivers.

For the year 1921 no data for sea temperatures are available. The air temperature in Stockholm was, however, above average every month from November 1920 to May 1921. March—April and May 1921 were especially warm. The salmon yield in 1921 was very good, as pointed out earlier, and the Norwegian salmon fishery had a peak the very same year (HUTTON 1930 b, SØMME 1948).

There are full data to prove that the temperature of the Baltic in the early spring of 1925 was again very high. According to DANNEVIG (1949), the surface water of the sea at Floedevigen, Arendal in south Norway was also very warm in 1925. DANNEVIG could prove by their scales that the growth of salmon in their first year at sea was rapid that year.

OLOFSSON (1926) reported exceptional abundance of small salmon in 1925 along the northern Swedish coast. They appeared as early as May. The salmon had had one or two years of sea life, judging by their scales, and some of them displayed very poor growth. If the cold spring of 1924 is supposed to have delayed the start of maturity and the warm spring of 1925 then accelerated it, a plausible explanation is found for the combination of two year classes in 1925, giving a larger population of small salmon and grilse than usual.

If growth was generally speeded up during 1925, more salmon would be »ripe» in 1926 and 1927 for starting their return journey. A peak in the salmon catch occurred in all countries in 1927, as was previously mentioned.

In the summer of 1930 the number of small salmon was again higher than normal along the northern Swedish coast (ALM 1931) but not until the summer of 1931 did the number culminate, their run then being exceptional (OLOFSSON 1932). Again the fish had one or two seasons of sea growth on their scales but had grown rather slowly. The spring of 1929 was cold, that of 1930 was very warm. Again two consecutive springs of very different character seem to have first delayed, then accelerated maturity, giving a combined run in late 1930 or the season of 1931. Most of the fish, running in 1931, probably had been at the coast as early as the autumn of 1930 since they were caught at the coast early in 1931, before the ice had gone.

In Norway too, the summer of 1930 was warm, giving a record rapid growth for the salmon then in their first year of feeding at sea (DANNEVIG 1949).

The warm spring of 1934 was again followed in the summer by a high salmon yield in the northern rivers. Very interesting is the fact that for three years, 1933, 1934 and 1935, DANNEVIG could report high water temperatures and very good salmon growth. This was followed in Norway, England, Scotland and Ireland by the general salmon peak in the years 1935—1937.

The warm spring of 1938 was recorded in the Baltic waters in March and

Table 4. Geographical variation in length of salmon sea life period in the Baltic.

River	Period in years of sea life, maiden fish							Average	Sample of fish examined
	A. +	A. 1 +	A. 2 +	A. 3	A. 4	A. 5	A. 6		
Sweden									
Mörrumsån (ALM 1924, 1934) .	—	56	278	1,005	39	—	—	2.75	1,378
Dalälven (ALM 1934)	—	1	39	145	28	—	—	2.94	213
Ljusnan (ALM 1934))	—	8	83	259	34	1	—	2.84	385
Ljungan (ALM 1934)	—	—	16	36	2	—	—	2.74	54
Indalsälven (ALM 1934)	—	4	145	184	16	1	—	2.61	350
Ångermanälven (ALM 1934) ...	—	11	161	220	42	2	—	2.69	436
Ume (ROSÉN 1918 b, ALM 1934)	—	8	76	197	15	—	—	2.74	296
Pite (ROSÉN 1918 a)	—	2	17	34	5	—	—	2.72	58
Lule (ROSÉN 1918 a, ALM 1934) .	—	76	95	128	39	—	—	2.38	338
Kalix (ROSÉN 1918 a, ALM 1934)	—	33	90	84	22	—	—	2.41	229
Finland									
Torne (JÄRVI 1938)	9	1,578	2,397	1,803	192	22	—	2.11	6,001
Kemi (JÄRVI 1938)	11	443	2,515	5,266	699	75	—	2.71	9,009
Oulu (JÄRVI 1938)	4	393	1,036	5,045	1,126	79	2	2.93	7,685
Kokemäki (JÄRVI 1938)	—	4	107	975	256	10	—	3.14	1,342
Kymi (JÄRVI 1938)	—	510	1,834	2,637	402	6	—	2.55	5,389

April but not later. It is interesting that the two most southerly Swedish rivers, the Mörrumsån and Klarälven, had a peak that very same year.

The effect of warm springs on the salmon run was observed very early. GISLER (1751 b) found the salmon peak years 1703, 1713, 1721, 1743 and 1749 all had two common factors: firstly, early and high floods in the rivers and, secondly, a warm spring with no ice in the sea or an ice cover that rapidly melted. Both the years 1747 and 1748 had small floods, but as there was no ice in the sea in the spring of 1748 the fishing was better!

Miss ESDAILE, (1913) found that the number of grilse was exceptional in the River Wye in the year 1911. She ventured to claim that »the excessive heat which accompanied the drought of the summer of 1911 may possibly have influenced the conditions of life of the salmon while in the sea and caused a hastening of sexual maturity».

JACOBSEN and JOHANSEN (1921) found statistically, that the number of salmon rising in the River Gudenaa fluctuated proportionately to the sea temperature one month earlier. If the water was warm, more salmon were caught and if the temperature was lower, the yield was less. The same phenomenon was observed by ALM (1924) in the River Mörrumsån.

The effect of the spring temperature on the sea-feeding salmon is analogous with the average length of sea life in the salmon. In the North Sea most salmon live for one or two years in the sea, while a minority stay for three periods of growth. In southern Norway the average life at sea is shorter than it is off northern Norway (DAHL 1910). In the Baltic most salmon live for two or preferably three years in the sea, which is longer on an average than the

Norwegian salmon at the same latitude (Table 4). Off the North American coast the atlantic salmon stays the longer in the sea the further north its home river is situated (HUNTSMAN 1938). Even the exceptions to this rule, giving the so-called »river races» of salmon, so much commented on in the literature, are, according to HUNTSMAN, paralleled by corresponding temperatures in the sea. On an average, therefore, it can safely be said that the colder the water the longer the salmon stays in the sea. This holds good both for geographical as well as annual differences. A cold year followed by a warm has, therefore, the most marked effect, the delaying action of the first year being added to the accelerating effect of the second giving a combined record run.

The effect of a cold sea in delaying the start of the run is sometimes hidden. The length of parr life is inversely correlated to length of sea life, as was already pointed out by Miss ESDAILE (1913), who discovered some of the most fundamental rules about salmon life. This principle was later confirmed by all the early authors (HUTTON 1918, ALM 1919, MENZIES 1921) but as DAHL (1910) had found a long parr life in the northern Norwegian salmon combined with a *long* sea life, he drew the conclusion that the rule was the reverse. Still later (DAHL 1937) he continued to oppose the principle that long parr life gives a short sea life, saying it was not evident from his Norwegian material. DANNEVIG (1949), however, demonstrated the inverse correlation for the Norwegian River Nidelven.

The length of sea life in the northern Baltic and in the northern Atlantic should, therefore, be short, as the parr stage is long. Where salmon from northern and southern rivers grow up together as in the Baltic Sea, the northernmost populations do in fact have a shorter sea life corresponding to their longer parr life (Tables 4 and 5). But when northern populations live in a colder sea than the southern ones, they have, in spite of their long parr life, a long sea life too. This cannot but stress the delaying effect of the cold sea on the determination of the time for return.

Therefore, summing up, it can be said that the statistical correlation between a mild winter and a subsequent rise in salmon yield during the next few years is probably due to the effect of high sea temperatures in spring on salmon run. More salmon »decide» to run during a warm spring giving a higher yield the same or next season. Moreover, since the growth is accelerated by the warm spring months more salmon speed up their growth and become capable of running in the next few years. These effects, on run and growth, combine to give the recorded peaks in the Swedish statistics. If a cold spring is followed by a warm one, their effects are added and the run, in the same or the next few years, is greatly increased.

Table 5. Geographical variation of smolt age in salmon in the Baltic.

River	Age of smolt in complete years					Aver-age	Sample of adult fish examined
	1	2	3	4	5		
Sweden							
Mörrumsån (ALM 1924, 1934)	104	1,141	133	—	—	2.02	1,378
Dalälven (ALM 1934)	—	134	77	2	—	2.38	213
Ljusnan (ALM 1934)	—	196	183	6	—	2.51	385
Ljungan (ALM 1934)	—	34	20	—	—	2.37	54
Indalsälven (ALM 1934)	—	140	206	4	—	2.61	350
Ångermanälven (ALM 1934)	—	143	285	8	—	2.69	436
Ume (ROSÉN 1918 b, ALM 1934)	—	124	161	10	—	2.61	295
Pite (ROSÉN 1918 a)	—	3	30	24	—	3.37	57
Lule (ROSÉN 1918 a, ALM 1934)	—	44	201	89	—	3.13	334
Kalix (ROSÉN 1918 a, ALM 1934) ...	—	24	152	52	—	3.12	228
Finland							
Torne (JÄRVI 1938)	—	100	4,258	1,737	97	3.30	6,192
Kemi (JÄRVI 1938)	—	820	7,443	1,255	35	3.05	9,553
Oulu (JÄRVI 1938)	—	1,152	6,155	726	12	2.95	8,045
Kokemäki (JÄRVI 1938)	1	1,373	228	3	—	2.14	1,605
Kymi (JÄRVI 1938)	28	5,216	711	5	—	2.12	5,960

The Delaying Effect of a Severe Winter

The Swedish salmon statistics indicated a peak in salmon yield after a considerable lapse of years, most often five years after a winter with severe ice conditions. It was also found, just as was the case with the maturing salmon, that the combined effect of a cold winter, immediately followed by a mild one, gave a record peak. This was the case for instance in the Svartö Weir in 1826, when the combined effects of the extremely different winters of 1821 and 1822 culminated.

The long lapse in years between the climate factor and its effect on the salmon yield suggests, of course, that climate influences the smolt transformation.

The transformation of the parr to the smolt stage is generally found to be delayed in low temperatures. DAHL (1910) was the first to point out the long parr life in northern Norway as compared to southern Norway. Miss ESDAILE (1913) found that the River Wye had still younger smolts than the rivers of southern Norway. Other British rivers fit into the scheme and she said: »It would, therefore, seem that the temperature of the water may have a considerable influence on the length of time the fish remain in the river. With the higher temperature there might be quicker growth and possibly a more rapid approach to the stage at which the young salmon are ready to go to the sea.»

For the Gulf of Bothnia ROSÉN (1918 a, 1918 b) found this principle at

Table 6. Average monthly temperature (Centigrades) in the lower part of some Swedish salmon rivers (from MELIN 1938).

River, locality and period	Month											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Torne, Juoksengi 1910-1918	—	—	—	—	—	10.5	16.4	13.9	7.4	—	—	—
Lule, Pajerim 1909-1925	—	—	—	—	3.8	10.8	15.7	14.3	9.1	1.9	—	—
Pite, Älvsbyn 1915-1918	—	—	—	0.1	3.1	10.3	16.3	15.1	8.4	1.9	0.1	—
Skellefte, Kusfors 1915-1919	—	—	—	—	3.9	8.9	15.3	13.9	8.0	3.2	0.3	—
Ume, Vännäs 1909-1935	—	—	—	0.1	4.7	11.3	15.7	15.3	10.3	3.9	0.5	0.0
Ångermanälven, Forsmo 1909-1920	—	—	—	0.4	3.8	11.1	16.6	15.2	10.3	4.4	0.8	—
Indalsälven, Ragunda .. 1909-1935	—	—	—	0.6	5.6	10.6	14.8	15.0	10.8	5.8	1.9	0.1
Ljungan, Torpshammar 1915-1931	0.6	0.6	0.6	1.7	6.5	12.5	17.4	16.2	11.2	5.5	1.8	0.6
Ljusnan, Framnäs 1913-1924	—	0.2	0.0	1.2	5.0	12.4	17.3	16.0	11.9	6.4	2.2	0.1
Dalälven, Älvkarleö ... 1917-1931	—	—	—	1.2	8.3	15.9	18.4	15.5	10.7	4.9	1.4	0.2
Mörrumsån, Mörrum .. 1910-1917	0.3	0.6	1.5	7.0	13.3	18.0	20.4	18.6	14.1	8.7	3.8	1.4
Klarälven, Edebäck ... 1910-1934	—	—	—	1.5	7.4	13.4	17.1	15.4	10.5	4.5	0.9	0.2

work and ALM (1919) confirmed the lower smolt age of salmon in the River Mörrumsån, running into the southern Baltic. Table 5 gives details regarding some Baltic rivers investigated. In Table 6 it can further be seen that the lower temperature in the more northerly rivers is actually verified. For North America the longer parr stage in the more northerly rivers has also been proved, according to the summary by HUNTSMAN (1938).

What happens then if a northern river is suddenly changed into a more southern one, or to put it another way, what happens to the parr in a warm spring or summer? The river temperatures may fluctuate widely in different years as shown in Table 7.

It seems rather probable that a warm spring accelerates the transformation of smolts, giving a good smolt class and, conversely, a cold spring or summer gives a subnormal transformation and a bad smolt class. The supply of growing parr, more or less at the stage where transformation might occur, could be increased after a cold summer and almost exhausted after a warm summer.

From the series of papers on the Wye salmon (HUTTON 1930 a, 1931, 1932, 1933, 1934), it can be seen that the water temperature in the spring of the years 1929, 1930, 1931 and 1932 was colder than average. HUTTON remarks that the number of smolts of higher age became more common in the catch from 1930 onwards.

The number of grilse was also progressively higher for several years, not only in the River Wye but in all British rivers. If the average age of the descending smolt increases, as a consequence of cold river water, more of them will return as grilse, according to the inversed correlation between the length of river and sea life. Finally, as the spring of 1933 was much warmer than average in the River Wye (HUTTON 1934) the stored supply of parr was probably exhausted by a heavy smolt class of 1933. This could be the explanation

Table 7. Selected annual variation of monthly mean temperature (Centigrades) in some Swedish salmon rivers (from MELIN 1938).

River, locality and year	Month											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Torne, Juoksengi 1918	—	—	—	—	—	8.0	15.7	13.5	8.2	—	—	—
Torne, Juoksengi 1913	—	—	—	—	—	11.7	18.1	13.9	8.1	—	—	—
Lule, Pajerim 1915	—	—	—	—	2.2	9.4	15.0	13.5	7.4	1.4	—	—
Lule, Pajerim 1925	—	—	—	—	6.3	12.9	19.6	17.6	15.3	—	—	—
Ume, Vännäs 1928	—	—	—	0.0	3.8	9.4	13.4	14.0	10.3	3.4	0.3	0.0
Ume, Vännäs 1930	—	—	—	0.5	7.4	13.0	17.4	17.5	10.2	4.2	1.6	0.0
Ångermanälven, Forsmo .. 1909	—	—	—	0.1	0.9	10.6	15.5	14.0	11.3	7.0	1.3	0.2
Ångermanälven, Forsmo .. 1914	0.0	0.1	0.0	0.6	4.5	10.9	18.3	15.4	10.6	4.6	0.4	0.5
Indalsälven, Ragunda 1909	—	—	—	0.6	1.7	7.7	13.0	12.8	10.7	7.4	1.6	0.0
Indalsälven, Ragunda 1930	—	—	—	—	8.0	13.3	17.5	17.9	13.1	6.5	—	—

for the exceptional rise in salmon yield in the River Wye and elsewhere in Great Britain in 1935 and 1936. It also corresponds to the size of the salmon in the different years.

In Norway, DANNEVIG (1949) found the percentage of grilse in the River Nidelven and at Arendal rose suddenly in 1926, i.e. the year following the warm summer of 1925 and again in 1931 after the warm summer of 1930.

WHITE (1939 b) found the actual descent of smolts to be stimulated by a rise in temperature and suggested: »As the young salmon do not descend until the time of transformation into smolts, and as it may confidently be assumed that this transformation is speeded up by temperature, it is reasonable to presume that with a higher temperature a larger number of the salmon reach the stage at which they are prepared to descend».

WILDER (1952) also thought temperature to be involved in the case of brook trout (Salvelinus fontinalis) where some populations are seagoing, while others are not.

Table 8 has been prepared from the extensive data published by JÄRVI (1938, 1948). The age of salmon smolts in two rivers is shown to have an annual variation, though the fluctuations are not significantly correlated. There is a trend in the Torne River data, showing a progressively lower smolt age for reasons unknown. It is suggestive that the highest smolt age in both rivers was recorded in 1929, a very cold spring.

The time that smolts descend in the Scandinavian rivers is not known very exactly. DAHL (1910) found it occurred in June in central Norway and in May in southern Norway. It occurs in April or early May in the River Gudenaa, Jutland (JOHANSEN and LÖFTING in HENKING 1916), mainly in April on the West-Coast of Sweden (EDMAN 1953, LAEVASTU 1954), and in April or May in the River Mörrumsån (ALM 1919). LING (1896 b, 1902) reported abundant smolts in August and September in the estuary of the River Indalsälven in 1895, and he observed smolts by the shore as late as October in the

Table 8. Annual variation of smolt age, as judged from scales of maiden fish ascending one to five years later. Derived from original data published by JÄRVI (1938, 1948).

Year of descending	River Oulu						River Torne					
	Age of smolt in complete years				Mean	Sample	Age of smolt in complete years				Mean	Sample
	2	3	4	5			2	3	4	5		
1922	29	140	7	—	2.88	176	—	—	—	—	—	—
1923	56	130	6	—	2.74	192	—	—	—	—	—	—
1924	45	671	28	—	2.98	744	—	—	—	—	—	—
1925	22	294	30	—	3.02	346	—	—	—	—	—	—
1926	38	340	30	1	2.99	409	—	—	—	—	—	—
1927	81	251	21	—	2.83	353	—	—.	—	—	—	—
1928	31	342	19	—	2.97	392	—	—	—	—	—	—
1929	69	691	157	1	3.10	918	8	488	358	9	3.43	863
1930	192	520	137	2	2.94	851	31	230	155	2	3.31	418
1931	133	961	80	—	2.95	1,174	12	1,261	168	1	3.11	1,442
1932	278	788	63	5	2.82	1,134	34	1,114	640	23	3.36	1,811
1933	234	1,118	71	2	2.89	1,425	14	1,033	374	56	3.32	1,477
1934	96	397	54	1	2.93	548	11	1,127	200	6	3.15	1,344
1935	40	248	9	—	2.90	297	21	245	83	—	3.18	349
1936	57	233	22	—	2.89	312	7	277	19	—	3.04	303
1937	97	408	25	—	2.86	530	31	987	141	1	3.10	1,160
1938	39	302	10	—	2.92	351	249	3,007	431	4	3.05	3,691
1939	51	108	—	—	2.68	159	220	1,794	128	—	2.96	2,142
1940	88	731	5	—	2.91	824	224	2,565	123	1	2.97	2,913
1941	18	114	4	—	2.90	136	23	579	20	—	3.00	622

Coefficient of correlation for Oulu and Torne rivers is 0.4781.
It is insignificantly different from zero. (P > 0.05).

year 1901. In a private communication, however, LINDROTH has informed the writer about more recent, unpublished investigations in River Indalsälven indicating smolt descent in June. He also suggested that some of LING's observations might have been on grilse. This category of ascending salmon is rare in all Swedish rivers and there is no Swedish word for them other than »små-lax» (small salmon).

A late descent into the Baltic could, if real, correspond with the fact that the sea is colder than the river up to August and may, thus, be an obstacle for further departure. Some tagged smolts (CARLIN 1955) have been found in recent years staying without movement and almost without growth by the shore for the winter, when released in the autumn. Some smolts, released in the spring, were found to be still at the same place one year later. Other fish from the same experiments, however, have moved away and grown larger as early as their first autumn in the sea.

It is important for future scale interpretation to know that JÄRVI and MEN-ZIES (1936), the most experienced salmon scale-readers of their time, wrote about difficulties in interpretation. Regarding the Baltic salmon, they point out that very often a »check» is engraved on the scales during the first year

of sea life. They say it may often be difficult to tell whether the salmon has spent this period of its life in the river or the sea!

A class of smolts start their sea life in summer, in autumn or the following spring and they return to the river after some years of feeding in the southern Baltic. The time for their return must be dependent on the actual weather that year, as discussed in the previous section. It is in the early months of the year that they »decide» to return. If they arrive at the home river before homothermy between river and sea in August, they rise the same season, if not, they must probably wait by the shore until the next spring. This may distribute them among the fourth, fifth and sixth summers after the original cold winter and spring. Since they become heavier the longer they stay in the sea, the yield, if recorded by weight, may very well represent a peak in the sixth summer. More up-to-date scale-reading especially on fish of known age and movement, is urgently needed to clarify this point.

The month of June, 1953, was exceptionally hot in Sweden. The supposed number of descending smolts should, therefore, be really large. LINDROTH has informed the writer that in 1954 (after a short period of heat in May) exceptional numbers of grilse were found in the River Indalsälven as also in other rivers. ALM (1955) found from statistics on the sea fishery that small salmon were abundant in southern Baltic in the autumn of 1953 and winter of 1954. The spring of 1955 was cold though the summer was very hot and few salmon ascended the northern rivers. If the spring of 1956 should be warm the salmon catch of the year ought to be good, if not, the peak is probably postponed until the year 1957.

The possible effects of severe winters on salmon predators are discussed below. This factor may stress those fluctuations already induced by climate, which always seems responsible for the small scale fluctuations of the Baltic salmon yield.

The Trigger Mechanism of Transformation

The discussion about salmon runs and smolt transformation has some bearing on the general problem of the timing of transformation phases in the life of fish, i.e. descent, ascent, onset of maturity and, finally, spawning, as they all are fixed in time in such a way as to occur in a biologically appropriate period of the year. The ultimate factor determining those processes in time must be selective survival, the best suited genotypes being the most common survivors.

Proximate factors, however, must have been evolved to fix the advantages evolved after selection. Of these, photoperiodism is almost certainly involved everywhere, being of major importance. In mammals and birds it has been found that photoperiodism, acting through the pituitary, functions as a guarantee that the behaviour induced by the right hormone should be displayed

at the right season. In fish, too, it has been proved, that photoperiodism gives the major time fixation for spawning, that is to say the start of the gonadotropic action of the pituitary (HAZARD and EDDY 1950). But the actual spawning behaviour is more closely controlled by a mechanism, where visual stimuli combine with temperature stimuli to release the actual pairing (FABRICIUS 1950). It was demonstrated (SVÄRDSON 1953) that the spawning period of whitefish was accelerated two weeks by unusually cold weather. This means that owing to photoperiodism a sensitive period is laid down, during which the fish has the capacity of reacting to purely environmental stimuli, e.g. temperature.

The trigger environmental stimulus, effective during a sensitive period and capable of releasing the start of gonadotropic action as the swelling of gonads, seems to be the temperature, at least in the case of salmon but probably in many other species as well. The start of sexual maturity has been very much discussed in literature (SVÄRDSON 1943, ALM 1946 for references) for its relation to growth rate.

Before going further into this problem, one definition must be made. The amount of developement achieved must be measured in a better way than by size or age, the two gauges most often used. The term needed may be called physiological age. If two specimens of fish are of the same age but not the same size, one has grown more rapidly. This specimen is more advanced in physiological age. If two specimens are of the same size but one is older than the other, having grown more slowly, it has the higher physiological age of the two.

Now, the known variability as regards the onset of sexual maturity and the »instinct» for migration in salmon, trout and eel could be more properly discussed with a set of hypotheses:

1. The time for the start of the transformation has an annual period of sensitivity or readiness (fixed by photoperiodism) within which environmental stimuli, e.g. the temperature may have a releasing effect.

2. The threshold of reaction is gradually lowered by the advancing physiological age of the fish. This means that for each consecutive annual period of sensitivity the amount of environmental stimuli, needed for releasing the hormonal drive or the actual behaviour, is lowered.

3. The environmental stimulus may be a change of temperature rather than a certain degree of temperature. Moreover, a more pronounced change has a stronger releasing effect than a less marked one. This means that a variation in the strength of the stimulus is allowed.

Let us see how this set of hypotheses may explain the plasticity of salmon. The general trend towards higher smolt age and longer periods of sea life to the north depends on the weak annual environmental stimulus, i.e. the low temperature or the slowly rise in temperature during the sensitive period. As

the physiological age proceeds, however, and the level of the threshold is lowered, even the weak environmental stimulus may be enough to induce the onset of smolt transformation or the gonadotropic processes, which accompany the return to the home river. Those fish which react latest are thus the biggest of their kind. The longest smolts, as well as the biggest salmon returning from the sea, are both found in cold northern rivers surrounded by cold seas.

Local variations in this pattern may easily occur. If the river is warm and the sea, in which the salmon moves, is also warm, we get the combination of low smolt age and short period of sea life. A near-by river may discharge its waters so that the descending salmon are driven into cold areas of the sea, where they remain for a long period. This river will be inhabited by big salmon. This simulates genetical »races» in different rivers, of which there is really very scanty evidence, not to speak of evidence to the contrary from a genetical and evolutionary point of view as well as experimental (cf. WHITE and HUNTSMAN 1938).

The writer would like to stress the opinion of SEDGWICK (1953) that the differentiation of early and late running salmon within the same river is also purely environmental. It was already suggested by ROSÉN (1918 a) that a high smolt age could be correlated to a birthplace very far upstream. GISLER (1751 a) stated that the later running salmon did not ascend as far upstream as the early runners did. The new fact, added by SEDGWICK, is that those fish, which were the oldest smolts, run earliest, and thus move furthest upstream, their progeny thus getting the smolt character of the parents though no hereditary trait is involved.

The onset of sexual maturity in salmon is earlier in the male than in the female sex. This is common for many species of fish. As a first consequence the sexual maturity of parr male salmon may be released by a temperature stimulus, which is not at all effective in releasing smolt transformation. In this way the male parr may spawn before the smolt transformation and then, in the sea, soon return again as grilse, yet again in account of the low threshold for the environmental release of gonadotropic function. The female may stay in the river for a number of parr years if her threshold for reaction is very high and — if the environmental stimulus is still too weak to function as a trigger, she may react like the male by the onset of sexual maturity while she is still a parr.

Such a case has recently been described for the norwegian River Namsen by BERG (1953). This is, of course, much more exceptional than the cases of landlocked salmon, where they have been »trapped» by interlocking lakes. In the Namsen, salmon are pure stream-dwellers. It is not known with any certainty if all the specimens stay in the river or if some of them — perhaps in a few warm years, according to the hypotheses put forward in this paper — are transformed into smolts. They fluctuate in number, which may indicate
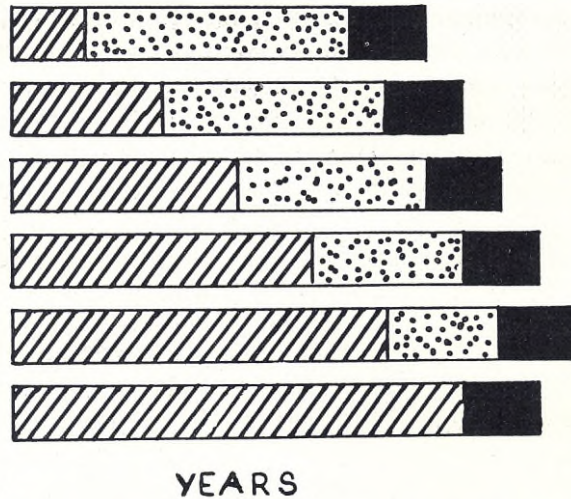
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YEARS

Fig. 3. Diagram to show the principal relation between the length of different stages in the life of the salmon and the environmental modification of this relation. Hatched: parr stage, stippled: sea life and solid black: spawning stage. The length of the postspawning period is neglected. It is suggested that when the stimuli for departure are deficient, the parr stage is extended, in exceptional cases so far that the sea life disappears entirely and the salmon becomes a stream-dweller as in the upper River Namsen, Norway.

that some are transformed into smolts. They live in the upper, and colder, parts of the River Namsen and are separated by high falls from the lower part of the river, famous for its abundant population of big salmon. Since this population is more dense than the spawning sites in the lower part of the Namsen could reasonably be expected to support, it seems rather probable, as suggested by BERG, that some of the abundant big salmon running the lower River Namsen have lived their parr life in the upper part of the river above the falls. If this is the case, the permanent stream-dwelling population in the upper Namsen may be really self-perpetuating only in the uppermost, coldest parts. The Namsen salmon are included in Figure 3 in order to show the principle advanced here for explaining their origin. Since their future life must be very much menaced by the present change in climate, it seems easy to understand why no populations of this kind have been found elsewhere. They must have had great difficulty in surviving the warm postglacial Stone Age. The sex ratio in upper Namsen ought to show preponderance of males.

The transition to the problem sea trout versus brown trout is not a very bold one. The parr-life period of trout in the Baltic rivers varies in quite a parallel way to that of the salmon (Table 9), though it is generally somewhat longer and may have a steeper geographical gradient. The difference between trout and salmon could, just as the difference between male and female salmon, be due to a different threshold of reaction as regards the onset of

Table 9. Geographical variation of smolt age in trout in the Baltic
(data from Järvi 1940).

Area	Age of smolt in complete years						Average	Sample of fish examined
	1	2	3	4	5	6		
Gulf of Bothnia	—	—	103	139	22	5	3.74	269
Gulf of Finland	—	19	19	2	—	—	2.58	40
The Archipelago of Stockholm	12	529	209	19	2	—	2.31	771
South Baltic	11	155	33	—	—	—	2.11	199

sexual maturity. The trout is the more »sluggish» species, needing a stronger environmental stimulus of temperature (and water velocity?) to make it react during the sensitive period of the year. The trend towards lowering the threshold (for smolt transformation) with advancing physiological age might also be slower. In this way the trout is easily »trapped» physiologically by sexual maturity like the male salmon. Dahl (1933) has described intermediate populations, where only an occasional specimen was a »sea trout», all the others being »brown trout». Trewavas (1953) published a new and excellent summary of the problem *Salmo trutta* systematics. The sudden disappearance of the migratory »instinct» in the third generation of sea trout bred in ponds, as described by Skrochowska (1953), probably means that the different migrations, performed by the tagged specimens, might be due to different environments in the river rather than to genetical differences between the lots of fish released.

In recent years the higher summer temperature (Liljequist 1950) might be responsible for the deplorable fact that brown trout populations in the small creeks of northern Sweden have generally decreased. In some cases the timber-cutting when all the trees in an area are felled, may give rise to a profound change in spring or summer temperatures in the creeks, where no shade is left. Regulations may have similar effects. In this way the departure stimulus of »non-migratory» trout populations may be affected and they descend and disappear. The sex ratio of stream populations often is very high.

Though genetical differences might, of course, occur between salmon populations as well as trout populations, it does not seem very probable that the sea going habit, where it differs between two populations, is really entirely genetic. At best it may be a slight difference in the average level of threshold reaction. Then the environmental stimuli must be reckoned with as the releasing factors.

Finally, a few words might be added on eel transformation from the yellow to the silvery stage. As is well-known, this transformation is related to that of the salmon and trout (Hoar 1951, 1953, Landgrebe 1941 Lynn and Wachowski 1951) and involves thyroid hormones. It was discovered by Jacobsen and Johansen (1922) that more yellow eels transformed into

silvery eels in a warm August than in a cold one. In northern Sweden (NORD-
QUIST and ALM 1920) the emigrating eels are very much larger than the speci-
mens further south. This is most probably a parallel to the larger smolts and
salmon in the north. Hitherto, it has been interpreted as being due to a sup-
posed better growth in the north (in a more sparse eel population) but this
postulates that the transformation should occur at a more or less fixed chro-
nological age in all the different regions. A delayed effect of the trigger
mechanism due to a deficient temperature stimulus during the months of
July or August seems more adequate as an explanation.

Salmon, trout and eel move from a hypotonic medium (fresh water) to a
hypertonic medium (sea water) and this is only possible if the osmoregula-
tion is changed. It is, therefore, interesting, and in line with the hypotheses
developed in this section that the complicated physiological processes, build-
ing up the mechanism of osmoregulation in fish, are temperature-dependent,
as proved by recent experiments (WIKGREN 1953).

The Great Periodic Fluctuations in Salmon Abundance

Hitherto only the modifying effect of temperature on salmon growth and
transformation has been discussed. It was found that the smaller fluctuations
in salmon yield could be paralleled to the effects of temperature. There is
another fluctuation in salmon abundance, however, which is of much greater
amplitude and this cannot be explained by an amalgamation of various birth
year classes to year classes of smolts and spawners.

The more rapid the growth the shorter the time available for predators
will be and the larger the number of surviving fish could be. The first pe-
riod of life in the sea may be especially important for survival. FOERSTER
(1944, 1954) demonstrated that the average size of the sockeye smolts was
larger the smaller their number and also that this slight difference in length
was followed by a significantly better rate of survival for the larger ones.
CARLIN (1955) found the same rule for survival in the atlantic salmon. More-
over, the severe winter could directly influence the rate of salmon predation
by reducing the number of predators.

Predators in fresh water and in the sea. HULT (1947) and HULT and JOH-
NELS (1949) released artificially-hatched salmon fry and studied the losses
from predation. It was found that perch (*Perca fluviatilis*) ate large numbers
of the young fry newly released.

STEINERT (1931) and OLOFSSON (1948) demonstrated that salmon fry
hatched in gravel cover was larger than that artificially-hatched. VIBERT
(1954) confirmed this and added that naturally-hatched fry could better
resist the predation of tested predators (eels). The territory of the young sal-

mon as well as its hidden life must play an important part in its early survival. This was proved by Mc CRIMMON (1954).

Therefore, it seems probable that the grayling (*Thymallus thymallus*) in the Swedish salmon rivers is the most serious natural salmon fry predator. TRYBOM (1908 b) found the grayling to be a predator of salmon eggs. After six years studying the spawning places of salmon, TRYBOM summarized that 257 graylings investigated had eaten 3,000 eggs of salmon or sea trout. He thought the grayling was capable of taking as many salmon eggs as were hatched in an average hatchery at that time. As the grayling is a permanent stream-dweller, it is still on the spawning grounds of the salmon when the fry emerge in the spring.

Pike and eel may be predators of salmon parr but their main habitat is different from that of the salmon.

The most serious predators of salmon parr seem to be mergansers. Two species occur in Sweden, the Goosander (*Mergus merganser*) and the Red-breasted Merganser (*Mergus serrator*). LINDROTH (1955 a, 1955 b) found both species preying on salmon parr. In Canada the mergansers have been found to be the most serious predators of salmon (WHITE 1936, 1939 a, REED 1953, KASK 1954). It is reported that merganser control was followed by a ninefold increase in smolt production.

The periodic decline in salmon yield in North American atlantic salmon has been interpreted by HUNTSMAN (1938, 1941) as being due to the predatory effect of king-fishers and mergansers in dry years.

The Canadian observations on mergansers were commented upon for British salmon habitats by HARDY (1954), who stresses that the balance between the salmon and its fish competitors may be disturbed by the merganser control practiced.

In the sea the salmon lead a pelagial life and as far as is known, are most preyed on by the seals and porpoises.

There are three species of seals in the Baltic Sea. The gray seal (*Halichoerus grypus*) is distributed over the entire sea but somewhat more sparsely in the far north. It is whelping on the ice in February and March. The season is at variance with that of the same species in the Atlantic. The whelping on the ice must be an adaption to the conditions of the Baltic Sea.

The ringed seal (*Phoca hispida*) is a species surviving from the postglacial arctic period of Scandinavia. It lives only in the northern Baltic, whelping on the ice in later winter. The Baltic subspecies is named *annelata*.

The harbour seal (*Phoca vitulina*) only inhabits the Southern Baltic, though it may live elsewhere in a very cold environment, i.e. off Greenland. It is whelping in summer by the shore. Probably competition between the two *Phoca* species accounts for their alternating distribution.

All the three species of seal are known to eat salmon, even from fishermen's nets, but the gray seal is the most serious predator, causing the greatest

trouble by its habit of visiting the fishing nets. MACINTYRE (1934) is of the opinion that the grey seal is more sluggish and therefore not such a serious menace to salmon. This may correspond with the Swedish observation that it is more a net-destroying species of seal, being in the habit of taking salmon from nets rather than in the open sea. In Scotland the harbour seal preys on salmon in the estuaries. Other species may also do that, as was the case in the autumn of 1747 when a flock of seals entered the lower part of the River Ångermanälven and preyed on salmon. The seals, grey or ringed ones, are reported to have stayed in the river at Sollefteå until the spring of 1748 (GISLER 1751 b).

Finally the last predator is the common porpoise, *Phocaena phocaena*. It has been argued that the porpoise probably does not catch salmon. MAC- INTYRE (1934) observed porpoises chasing salmon and reports fishermen's observations according to which porpoises may catch salmon in the open sea. EKMAN (1938) reports a flock of porpoises (at Kramfors) some way up- stream in the River Ångermanälven in the summer of 1915, most probably in pursuit of salmon.

This whale migrate through the Danish sounds into the Kattegatt and Skagerack in the winter and returns to the Baltic in spring. This is verified by a traditional form of hunting in the sounds and off the southwest coast of Sweden in older days, when train oil was of some importance.

The influence of a hard winter on the salmon predators. Fish are probably not much influenced on the whole by a hard winter. It is recorded that eel may die in large numbers in cold winters (JOHANSEN 1929) but as this occurs in the sea it may be a special case of imperfect adaption to Saline conditions.

Mergansers may suffer some extra losses during a hard winter but there are no records of it. The official statistics concerning shot mergansers (Table 10) are a bad gauge for trends in population. They are not exact and may some years include large numbers of mergansers shot in Bleking, when they are passing along the coast on their way towards Finland and Russia. Nevertheless, it seems justifiable, to reckon with a somewhat higher mor- tality than normal for the mergansers during a severe winter. Most of them winter in the Danish sounds but some may fly to the British Isles as ringed specimens have done.

The statistics concerning shot seals (Table 10) have been discussed by HULT (1943), ECKERBOM (1948), and LINDROTH (1950). The trend is down- ward, but this is due in the main to the fact that almost all seals formerly killed were hunted by professional seal-hunters. This is no longer profitable from an economic point of view and the number of seals killed has, there- fore, fallen. Nevertheless, ECKERBOM and HULT think the decrease in ringed seals is genuine, as they have disappeared from their southern marginal area of distribution. This decrease has, however, been due to the improvement in climate, the fact that the winters have been milder. Thus there is no evidence

Table 10. Number of seals and mergansers killed in Sweden.

Year	Gray seal	Ringed seal	Harbour seal	Seals	Mergansers
1902	—	—	—	4,087	—
03	—	—	—	5,823	—
04	—	—	—	4,681	—
05	—	—	—	3,796	—
06	—	—	—	5,033	—
07	—	—	—	6,141	—
08	—	—	—	7,347	—
09	—	—	—	6,476	—
1910	—	—	—	8,935	—
11	—	—	—	7,505	—
12	—	—	—	7,191	—
13	—	—	—	8,619	—
14	—	—	—	2,967	—
15	—	—	—	3,271	—
16	—	—	—	3,889	—
17	—	—	—	4,475	—
18	—	—	—	6,071	—
19	—	—	—	6,596	—
1920	—	—	—	3,365	—
21	—	—	—	2,399	—
22	—	—	—	3,774	—
23	—	—	—	3,671	—
24	709	2,228	116	3,053	—
25	1,362	2,605	131	4,098	—
26	733	2,437	137	3,307	—
27	834	2,345	138	3,317	—
28	790	2,118	136	3,079	—
29	1,241	3,580	186	5,007	—
1930	1,713	5,934	249	7,396	—
31	961	2,380	177	3,519	—
32	2,275	2,189	363	4,828	—
33	1,240	2,791	215	4,246	—
34	2,368	2,050	174	4,592	—
35	748	1,541	214	2,503	—
36	766	1,617	192	2,588	—
37	384	1,139	152	1,675	—
38	766	813	142	1,721	—
39	731	1,428	129	2,288	—
1940	418	602	110	1,130	—
41	250	318	110	678	5.000
42	466	584	135	1,185	10,000
43	850	993	116	1,959	11,500
44	—	—	—	2,786	11,000
45	—	—	—	1,876	13,000
46	783	1,016	88	1,887	9,000
47	615	876	84	1,576	11,000
48	783	949	104	1,786	10,000
49	707	637	99	1,443	10,000
1950	480	405	86	971	9,000
51	397	221	88	706	5,000
52	—	—	—	533	6,000
53	203	273	56	532	6,500

that severe winters may be dangerous. Both the ringed and the gray seal whelp on the ice but the ringed seal always keeps a hole open, so it can disappear into the sea if disturbed. The gray seal, however, has not the same habit of always keeping a hole open and in a severe cold spell, it can be

isolated on the ice and killed by hunters (LÖNNBERG 1898, ECKERBOM 1948). Sometimes great flocks may be killed, as in March 1896 when more than 500 mostly young gray seals were killed off the coast of Västernorrland in the Gulf of Bothnia (LIND 1896 a). This mortality, however, is caused by *ice and man* together and not by the ice alone.

The harbour seal is not known to suffer either but it is said that it cannot keep holes open in the ice as the ringed species does (ECKERBOM 1948). Some winter mortality may, therefore, occur.

As regards the porpoise, matters are very different. This is the only salmon predator, which is really sensitive to severe winter conditions. Normally it moves out from the Baltic to warmer waters in winter and returns in spring (MØHL-HANSEN 1954) but as there is more likelihood for freezing in the sounds than in the southern part of the central Baltic (JURVA 1952) some or more may be caught by the ice and trapped in the Baltic. It may prove very dangerous for them.

In 1924 hundreds were drowned by the ice-sheet off Bornholm and the carcasses were later found in spring by fishermen (JOHANSEN 1929). Probably the very same winter a flock of roughly a hundred porpoises were driven by a large ice-belt into a bay, Kapellshamnsviken, in northern Gotland. The ice cut off all possibility for them to return back to the open sea and all of them were drowned (EKMAN 1938, LÖNNBERG 1940).

A heavy porpoise mortality occurred in 1929 in the waters off Bornholm. In the spring the fishermen saw hundreds of dead porpoises floating on the surface of the sea and quite a number of rotting carcasses appeared in the trawls. Some were »fished» up from depths of 90—100 metres. Not a single dead seal was seen (JOHANSEN 1929).

Again in 1940, when the total area of sea was frozen, a great many porpoises must have been trapped in the Baltic. In the spring hundreds floated inland to the east coast of Skåne with easterly winds and at Fårö, the north point of Gotland, hundreds were found dead and lay rotting on the shore the whole summer (ALANDER 1940, LÖNNBERG 1940).

These, of course, may be only small items of information as to what really happens in the sea, when large areas of the Baltic are covered by ice. Though it has been difficult to record exact extent, porpoise mortality in some severe winters is definitely proved. If porpoises normally catch a significant number of salmon in the sea, this hard winter mortality should be registered by a rise in the salmon yield during subsequent years. There is also the further possibility that migrating porpoises return later to the Baltic in those springs, when the water is cold. If the porpoises catch considerable numbers of small salmon just arriving at the southern Baltic from the north for their first season of growth, an extra month of reduced predation may be important. It might be remembered that FOERSTER (1944, 1954) found survival in the sea positively correlated to small increments in the size of descending smolts.
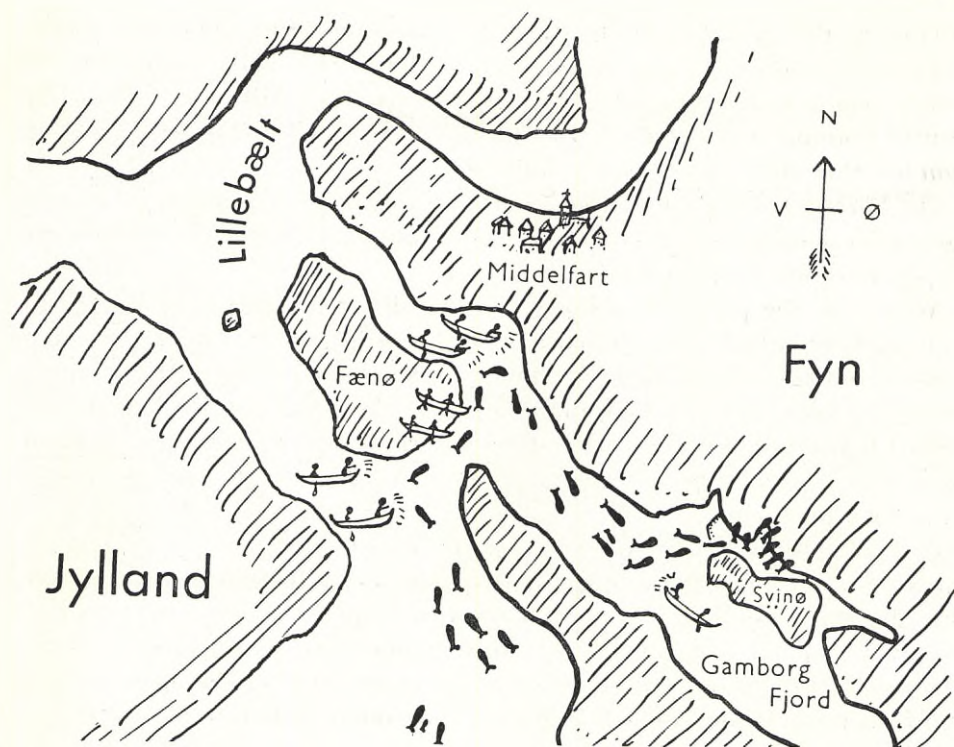
Fig. 4. Map of Lillebaelt in Denmark and sketch to explain how the porpoises are caught at Gamborg Fjord (after Møhl-Hansen 1954).

As the salmon yield in fact rises after severe winters and, moreover, generally is higher in a period when the Baltic is often frozen, a correlation seems possible. As was stressed by Shapovalov and Taft (1954), mortality due to predation seems more probable for seagoing salmon than mortality from disease or food shortage. But the evidence of an inverse correlation between the populations of Baltic porpoise and Baltic salmon is still more suggestive. When the porpoises migrate from the Baltic in the autumn, they are concentrated in the narrow sound between Jylland and the Isle of Fyn. Since ancient times they have been caught in the late autumn at a place near the town of Middelfart. The method is described by Møhl-Hansen (1954), who says some legislation regarding this hunting dates back to mediaeval times (Figure 4). The name of the small isle, where the porpoises are finally hauled ashore, is Svinø, referring to the Danish name for the porpoise. The record catch is said to have been 3,000 porpoises in a season, but the normal annual catch was usually between one and two thousand (Ekman 1938). This appears to be a considerable rate of mortality for the Baltic stock of porpoises, as the female only bears one young per year.
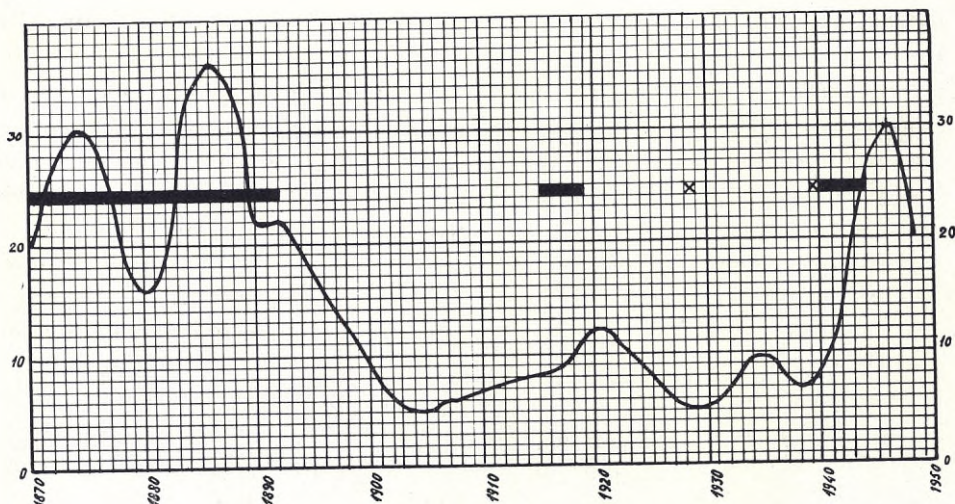
Fig. 5. The Swedish salmon yield 1870—1950 and the occurrence of porpoise-hunting in Denmark (the black horizontal bar). Note that the three periods of porpoise-hunting all were accompanied by a higher salmon yield. Heavy porpoise mortality due to ice occurred in 1929 and 1940.

If the porpoise had some influence on the Baltic salmon stock, the fluctuations in the Danish porpoise-hunting at Middelfart should have an influence on the yield of salmon. According to MØHL-HANSEN (1954) the porpoise-hunting, which had been practised for centuries, was stopped in 1892 owing to low prices for train oil. It is very suggestive that this was immediately followed by the catastrophic fall in salmon yield in the late 1890's in the Baltic! Ten years after the termination of the Danish porpoise-hunting, in 1902, it was pointed out by one of the salmon experts in Sweden (LING 1903) that porpoises had become much more common on the Swedish coast in the Gulf of Bothnia of recent years. Some porpoises were caught and more specimens were observed. LING believed that they did great damage to the salmon!

The Danish porpoise-hunting at Middelfart was again practised in 1916—1919. This porpoise-hunting was followed by a great rise in the Baltic stock of cod in 1919—1921 (HESSLE 1923 b) and by a distinct peak for salmon in 1920—21.

Finally, in the years 1941—1944, porpoise-hunting was again practised at Middelfart. MØHL-HANSEN (1954) obtained about 700 animals to study but no statistics are available regarding how many porpoises were actually killed. Nevertheless, it again corresponds with the steep rise in the salmon population of the Baltic noticeable from 1941. The number of porpoises drowned in 1940 may have been really large.

The surprisingly coincident rise of porpoise mortality (whether natural or artificial) and salmon yield is very suggestive (Figure 5). It may be a case of

a predator affecting a prey species to a much greater extent than is normally the case (ERRINGTON 1946, LACK 1954). From a theoretical point of view this prey-predator relationship may illustrate a balance occurring in a case where there are no food or space restrictions for the prey species, since these compensatory factors can mainly operate on salmon in fresh water but not in the sea. From a practical and commercial point of view the consequences may be far-reaching. Since it has already proved possible for a few men to catch thousands of porpoises a year merely for selling the train oil, it must be possible in modern times to trap at least the same number with modern gear, especially if this practice saves hundreds of thousand *kronor* for the salmon fishermen of the Baltic.

The relation between porpoise and salmon can be and ought to be tested by an experiment. The porpoise-hunting tradition of the citizens of Middelfart must be revived and as many of the migrating porpoises as possible caught for some years, so as to see what happens to the salmon in the Baltic. If the reaction is once again positive a method has been found for conserving in the Baltic a permanent salmon population more abundant than the present one.

Summary

1. From data on ice conditions in the Baltic a statistically significant correlation between the area of maximum ice cover of the Baltic Sea and the salmon yield five years afterwards is proved.
2. Two or three years after a mild winter another peak in salmon yield is achieved, which is also statistically significant.
3. It is found that the annual temperature conditions in the sea and the rivers give a fluctuating salmon yield by means of »smolt classes» and »spawning classes», which are not parallel to the ordinary birth year classes. This is the biological foundation for the correlations mentioned above.
4. A set of hypotheses is given, according to which transformations in fish, whether from nonmigratory to migratory or from unripe to ripe conditions, can be explained. A trigger mechanism, where a temperature stimulus is the releasing factor acting only during a certain sensitive period, is involved in all cases. The threshold of reaction sinks with the advancing physiological age of the fish. The sensitive period is fixed by photoperiodism.
5. The variations in salmon yield caused by temperature fluctuations are accentuated by the effect of severe winters on salmon predators. A slight effect may be obtained in fresh water but the main effect is in the sea, due to interference with the common porpoise, *Phocaena phocaena,* a species which is very sensitive to hard winters and has repeatedly suffered great losses in winter.

6. It is pointed out that the termination of the ancient Danish porpoise-hunting at Middelfart in 1892 coincided with the catastrophic fall in salmon yield in the Baltic in the 1890's. The porpoise-hunting has twice been practiced again for a short period of years. Both periods have once more coincided with a rise in the salmon population, one of the periods giving a peak for the cod population of the Baltic as well.

7. It is suggested that the relations between the Baltic salmon and the porpoise should be further studied by an experiment. When the Danish porpoise-hunting is revived, it will take only a few years to see if the salmon stock will again react.

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