Nils Rosén

INSTITUTE OF FRESHWATER RESEARCH, DROTTNINGHOLM
REPORT No 35
FISHERY BOARD OF SWEDEN

ANNUAL REPORT

FOR THE YEAR 1953

AND

SHORT PAPERS

LUND 1954
CARL BLOMS BOKTRYCKERI A.-B.

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Director's Report for the Year 1953

By Sven Runnström

Members of the Staff in January 1954

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Gunnar Svärdson, fil. dr.
Thorolf Lindström, fil. dr.
Eric Fabricius, fil. dr.
Karl-Jakob Gustafson, fil. kand.
Maj Stube, fil. kand.
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Laboratory Assistants: Ingrid Johannisson
Solveig Andersson
Gunnel Nordebäck
Porter: Henning Johanson, Algot Sjölander
Kälarne Research Station (in the Province of Jämtland)
Fishery Assistant: Elof Halvarsson

The Director was away on leave of absence in the autumn of 1953 for three months to make a journey for the purposes of study to the U.S.A. and Canada. Dr. Brundin has also been away on leave during the latter half of the year on an expedition to South America and fil. kand. NILS-ARVID NILSSON has deputized in his stead. Dr. KARL MÜLLER has been temporarily employed at the Institute for special investigations. As may by seen in the list of personnel, the staff has been increased by three new fishery assistants. ANDERS TÄGSTRÖM has, in addition, been employed as extra laboratory assistant. 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.

The porter, Mr. JOHANSSON was ill during the whole year and was replaced by Mr. SJÖLANDER.

Scientific and Practical Work by the Staff

BRUNDIN started at the end of July on a journey of exploration to South America together with two other biologists for limnological investigations in the Andean Lakes of Chile and Peru. The purpose was a comparison of lakes in the Northern and Southern Hemispheres.

NILS-ARVID NILSSON has, during BRUNDIN's absence, begun an investigation of the relations between the food available in a lake and the feeding of the fish, partly with material previously collected by A. MÄÄR in the River Faxälven (Province of Jämtland) during the years 1944—1949. The chief interest has been concentrated on the feeding habits of the char and trout and during the course of the work three main problems have appeared:

1) The temporary variation in the fishes' choice of food and its causes.
2) Competition for food between char and trout and their ecological niches.
3) The effect of damming up lakes on the feeding habits and growth of the fish.

The material available has shown that the feeding habits of the fish vary very considerably not only seasonally but also from year to year. A certain regular rhythm can be discerned however. In the char this is characterized by a variation between bottom animals (winter), flying and hatching insects (spring and summer) and zooplankton (summer and autumn). The primary food of the trout consists of bottom animals with a considerable addition of flying and hatching insects during the late summer. A closer analysis of the forms included in the food of both the species of fish does not suggest that there is any substantial competition for food between the two species in this lake. Lake Blåsjön was regulated in the year 1949 by damming up the water level during the summer and by lowering it during the winter. The material studied originates partly from the years before regulation, partly from the first year regulation took place. It has not been possible to discover any change in the feeding habits of the fish, which definitely could be interpreted as being caused by the regulation. A decided increase in the proportion of zooplankton in the char's food during the year regulation occurred is possibly such an effect, but can just as well be thought to depend on other factors. Further light should, however, be shed on this problem after the study of additional material from Lake Blåsjön and other mountain lakes, which is to be collected during the year 1954.

As the other investigations included in the program of the Institute are of a long-term nature, they have mainly consisted during the year of a continuation of the previous year's investigations, which were described in the last report, and I shall now only give a brief account of some of them.

Collection of material for SVÄRDSON's whitefish investigations was intensified during the autumn of 1953, a more convenient method than the earlier one being employed. Previously whole fish were bought from fishermen or sent in by fishery assistants belonging to the Institute. Since it became increasingly clear that the proportions of the body and the more general measurements were of no use for identifying species, material collection has been simplified by taking scale samples and particulars of length in the field, after which the cutted heads, with a number corresponding to that on the scale bag, were sent in to the laboratory where the gillrakers were counted and the scales read. The fishery assistants as well as the local fishery officers took part in the collection of material. The gillrakers of the entire material could, furthermore, be worked up by degrees at about the same speed as it came in. An extra assistant, Mr. TÄGTSTRÖM, was employed for this purpose. This contribution augmented the whitefish material with not less than 4,256 specimens examined, which constitutes an increase of more than 50 % of the total material during the year.

SVÄRDSON has also continued the collection of scale samples of pike during the year. As a first working up of the material collected (scale samples from approx. 40,000 pike), scales have been examined from about thirty pike whose age is definitely known, as they were planted out as fin-cut fingerlings. This investigation showed that the age of these pike, if it had not been known, would have been estimated as being higher than it was in reality. This serious drawback bas been the cause of considerable anxiety. The principles on which the scales of pike are to be interpreted seem to be less clear than was previously supposed. The reasons are mainly that the pike seem to grow rather uniformly throughout the year with relatively inconsiderable seasonal variations and, in addition, that as yet unknown factors vary individually and cause a number of false »rings». A great deal more basic studies of the interpretation of pike scales are needed before working up of the large scale material can be commenced.

In the autumn of 1953 an electric cooling apparatus was installed in the aquarium at the Institute, making it possible for FABRICIUS to continue his studies of the spawning behaviour of the char under better conditions than previously. Territorial behaviour and the females' selection of nest sites were studied amongst other things in a seven metres long aquarium, where several pairs of char could spawn simultaneously. Stimuli releasing aggressive behaviour in the males were investigated by means of experiments with models and several new details in the spawning behaviour were observed.

The spawning behaviour of the char was recorded by K.-J. GUSTAFSON in a 16 mm. colour film, which made it possible to analyse in detail nest-digging movements and the apparent trembling movement in the courting. A detailed account of the char's behaviour can be found elsewhere in this volume.

FABRICIUS has also collaborated with Dr. ARNE LINDROTH in studying the spawning behaviour of the whitefish in an aquarium with running water at the laboratory of the Migratory Fish Committee at Hölle. An account of these observations is included in this report. In addition FABRICIUS has continued his observations on the behaviour of young salmon, brown trout and char. These investigations have been extended to include brook trout, rainbow trout, whitefish and grayling as well as hybrids of char and brown trout resp. brook trout. These experiments have partly been carried out in running water at the Hölle laboratory partly in still water in the aquarium at the Institute.

During the autumn of 1952 FABRICIUS marked char on spawning grounds in Lake Borgasjön. In the autumn of 1953 Lake Borgasjön was dammed up 18 metres above normal water level for the first time and test fishing was carried out during the spawning season to determine whether the char had changed their spawning habits. A number of marked char were recaptured at the same spawning ground, where they had been marked the previous year, in spite of the depth now being 18 metres greater. Other marked char were, however, caught in the inflowing river, the Sannarån, or on spawning grounds in Lake Sannaren and Lake Raukajaure above Lake Borgasjön. The char can consequently either spawn in the lake, where they are living, migrate up a river and spawn in running water or migrate through the river system up to other lakes and spawn there. The same specimens, which have followed one of these three behaviour patterns one particular year, can change next year to another one if the external conditions are altered.

Control of different fish populations of salmon, trout, char, grayling and whitefish in weirs has been continued to the same extent as the previous year. Regarding the spawning migration of the trout from Lake Storsjön to the River Dammån (Province of Jämtland), 559 specimens passed through the control at the fish ladder this year. The average weight of the fish was 2.3 kg. and the distribution according to sex was 252 ♀♀ : 100 ♂♂. The greatest ascent occurred in July and August. The ladder was examined and emptied every fourth hour and the greatest migration upstream during the day and night took place in the morning at eight o'clock and in the afternoon at four o'clock. At night the amount ascending the ladder was inconsiderable. All the fish (559 specimens) were marked and of these 57 were reported as recaptured in the river and 10 specimens in different parts of Lake Storsjön the same year. 161 of the fish controlled in the ladder had been marked during previous years. 111 of these fish had been marked in the year 1951, from which it seems apparent that the majority of the fish seem to spawn every other year. 23 fish had returned to spawn after 3 years and 19 had spawned during at least two consecutive years. One of the latter fish had even spawned during four consecutive years.

KARL MÜLLER's investigations concerning the effect of clearing floating ways on the production of nutriment in running water have been concluded during the year and an account of the results is given in a paper in this report. During the course of the investigations MÜLLER became aware of the great importance of the organic drift as fish food in running water and this problem is dealt with in a special paper in this volume.

The test fishing with nylon carried out by MOLIN in 1953 was of two kinds. One was a direct continuation of previous experiments on the variations in the fishing capacity of the nylon nets in different light conditions and different degrees of turbidity in the water. Test fishing took place in two localities, namely Lake Locknesjön in Jämtland with a depth of visibility of 12 m. and Lake Sillen in Central Sweden, where the depth of visibility was 1.2 m. The results further emphasized the superior fishing qualities of nets made from monofilament nylon as compared with nets made of cotton and spun nylon. The greater catches with the monofilament nylon were particularly noticeable during the times of the year with the most daylight. — The other experiment was carried out in Lakes Vänern, Vättern, Mälaren and Hjälmaren using the same type of nets as are used by commercial fishermen in these lakes. At the beginning of 1953 there was no good supply of satisfactory nets made of monofilament nylon, and in the nets used the knots were of poor quality, so the results were misleading to a certain extent. In spite of this about twice as many fish were caught in Lakes Vänern and Vättern with the monofilament nylon nets as with nets of spun nylon and in Lake Hjälmaren 3 times as many fish as with spun nylon. The test fishing in Lake Mälaren was a total failure, as the knots on that net were very prone to slip. During 1954 the test fishing is to be continued with more suitable nets.

The experiments on the effect of ultraviolet radiation on cotton yarn, spun nylon and monofilament nylon were concluded during 1953. After radiation for a certain length of time with ultraviolet rays the resistance to tearing of the cotton yarn had decreased by 66 %, spun nylon by 84 % and monofilament nylon by 29 %. The last mentioned material thus proved the most resistant to ultraviolet radiation.

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Rep=Report from this Institute.

SFT=Svensk Fiskeritidskrift (Swedish Fishery Journal). Only Swedish language.

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BERG, S. Bekämpande av ogräsfisk. *SFT 62: 108—110.*

BERG, S. and STARK, R. Fiskar och fiske i Ångermanlands och Medelpads sjöar och kustvatten. *Natur i Ångermanland och Medelpad, Svensk Natur, Stockholm.*

BRUNEAU, L. Om vattenprovtagning. *SFT 62: 7—12.*

— Några resultat av vatten- och bottenundersökningar vid Ångermanlandskusten. *Sv. Papperstidning Nr. 6/1953: 1—10.*

CARLIN, B. Märkning av utvandringsfärdiga laxungar. *SFT 62: 57—59.*

— Behandling av laxrom med malakitgrönt. *SFT 62: 191—192.*

EDMAN, G. En laxundersökning i Halland. *SFT 62: 66—70.*

FABRICIUS, E. Aquarium observations on the spawning behaviour of the char, *Salmo alpinus* L. *Rep. 34: 14—18.*

— Laxöringen. *Lax och Öring. Stockholm.*

— Rödingen. *Lax och Öring. Stockholm.*

— Fiskarnas sinnen. *Lax och Öring. Stockholm.*

FABRICIUS, E. and K. J. GUSTAFSON. Rödingens lekbeteende. *Sv. Faunistisk Revy 15: 124—131.*

LAEVASTU, T. Gasblåsesjuka i fiskodlingarna. *SFT 62: 127—129.*

— Några elfiskeundersökningar i Lagan, Smedjeån och Stenån. *SFT 62: 152—156.*

— Om storlekssorteringens inverkan på könskvoten hos laxungar. *SFT 167—168.*

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LÖFFLER, H. Beitrag zur Planktonkunde des Faxälv-Systems. *Rep. 34: 58—72.*

MOLIN, G. Test fishing with nets made of monofilament thread. *Rep. 34: 73—77.*

— Fiskeförsök med nätredskap tillverkad av heldragen nylontråd. *SFT 62: 53—56.*

MÜLLER, K. Die Schuppenmissbildungen bei der Forelle, Salmo trutta L., und eine Deutung dieser Erscheinung. *Rep. 34: 78—89.*

— Produktionsbiologische Untersuchungen in Nordschwedischen Fliessgewässern. *Rep. 34: 90—121.*

— Undersökningar över fiskbeståndet och dess näringsgrundval i traktorrensade flottleder. *Sv. flottledsförbundets årsbok.*

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STJERNA-POOTH, I. Die Kieselalgenvegetation in zwei azidotrophen Seen des Küstengebietes von Nordschweden. *Rep. 34: 122—140.*

SVENONIUS, B. Behandling av rom med malakitgrönt. *SFT 62: 192—193.*

SVÄRDSON, G. The Coregonid problem, V. Sympatric whitefish species of the lakes Idsjön, Storsjön and Hornavan. *Rep. 34: 141—166.*

— Metoder i fiskodlingsfrågan. *SFT 62: 2—5.*

— Fiskeristatistik i Svensksjön. *SFT 62: 26—28.*

TÖRNQUIST, N. Dalslands sjöar, fiskar och fiske. *Natur i Dalsland, Svensk Natur, Stockholm.*

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Maturity, Mortality and Growth of Perch, *Perca fluviatilis* L., grown in Ponds

By Gunnar Alm

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Introduction

In some species of fish, primarily perch (*Perca fluviatilis* L.) and pike (*Esox lucius* L.), the larger specimens mainly consist of females. This is due, as a number of scientists have shown, to the rate of growth in the males decreasing more rapidly than in the females, which is sometimes placed in conjunction with the males reaching sexual maturity earlier than the females. It is also often stated that mortality from natural causes is higher in the males. On the other hand it is a well-known fact that the great majority of fish caught during the spawning season are males. This is especially true as regards populations of stunted perch, where sometimes as many as 80—90 % of the fish captured during spawning are males (Alm 1951). The explanation for this is thought to be that the males are more active during spawning and that they remain on the spawning grounds a longer time than the females.

For the last few years experiments concerning the above mentioned questions have been carried out at the Kälarne Fishery Research Station. The experiments have been concerned with perch and trout, and to a certain extent other species as well. Only the results obtained up to now in experiments with perch will be dealt with here.

Material and Methods

All the experiments have taken place in ponds at the Kälarne Fishery Research Station. The ponds are generally 7—8×70—90 metres in size, that is to say 500—700 square metres. Their depth amounts to 1—1.5 metres. They all have relatively rich vegetation of different *Potamogeton* species, *Polygonum fluitans, Glyceria fluitans, Myriophyllum, Batrachium* etcetera and they also have a well-developed vegetation fauna. To a certain extent they could, therefore, be considered as representing very small natural bodies of water. Some ponds are larger, more irregular and shallower, but otherwise of a similar nature. Other fish such as trout, grayling, whitefish, brook trout, roach etc. have also been kept in the ponds as well as the perch. Efforts have been made, however, to have only fish of about the same size as the perch. No greater decimation through predatory fish has occurred.

Every spring and autumn, usually in the middle of May and the beginning of October, the ponds have been emptied and the fish examined as regards number, size, sexual maturity and spawning etc. Every spawning group, that is to say the specimens of each sex taking part in the spawning for the first time, have been kept apart by marking (cutting a certain fin). In this way it has been possible to follow year by year the growth and loss of a certain group, as well as to discover whether the spawning takes place annually or only with certain intervals. This method of marking has not, as far as could be observed, had any injurious effect. When rendering an account of the number of fish examined, it is sometimes found that there is a larger number at a later examination than at an earlier one. This depends on difficulties in getting out all the fish from the pond. Some specimens could be left in the pond and be included the next time. With a view to obtaining populations with better or poorer growth, the number of specimens in the different experiments varied very much, which is also the case with other fish in the same ponds. In this way it has gradually been possible to get several populations, the majority with moderately good although varying growth, one on the other hand with decidedly bad growth.

Results

Sexual Maturity

Figures showing the number of sexually mature males and females in connection with increasing age are to be found in Table 1, summarized for the entire material. In the experiments now under discussion no perch was sexually mature at the age of one year. At two years of age sexual maturity was attained by a number of males. 231 specimens or 13 % out of 1,741

Table 1. Age and sexual maturity of perch in ponds. Age is recorded in full years, i.e. the fish were studied in May, at the spawning time.

Age in years	Ripe ♂♂			Ripe ♀♀			Immature		Total number of specimens
	Number	%	Number spawning first time	Number	%	Number spawning first time	Number	%	
2	231	13	231	—	—	—	1.510	87	1.741
3	559	46	390	1	(—)	1	666	54	1.226
4	463	48	45	85	9	85	407	43	955
5	325	50	22	203	31	130	121	19	649

perch consisted namely of males ripe for spawning the first time. Such specimens then occurred annually, but mainly at three years of age, when the total number of spawning males consisted of 46 % of the entire total of specimens. At 4 years of age the number of new sexually mature males was far less, and at 5 years the number of such specimens was only 22. All the males, 50 % of the entire number of specimens, have now clearly reached sexual maturity. Practically all the males have spawned year after year, after they had once attained sexual maturity. Only 6 specimens did not spawn a further year.

Only one of the females was found to be sexually mature at the age of three years. At four years at least 85 females had begun to spawn, and at five years of age a further 130 females were spawning, and only 121 specimens had not yet reached sexual maturity. It is probable that all these consisted of females — some specimens that were examined showed this to be the case — that would spawn for the first time the next year. The females have thus become ripe principally at five years of age and after that at six years of age (not yet reached in these experiments). The females too, with a few exceptions, spawned every year.

The number of males spawning at five years of age totalled 325, and the number of spawning females of the same age as well as specimens not yet sexually mature, probably all females, was 324, so the sexual ratio was 1 : 1.

Mortality

If the first year is disregarded, when mostly very great losses occur, out of 3,690 one-year-old specimens there were 1,741 specimens left the next spring or 47 %. During the following three years the losses were less, especially during the fourth year (Table 2) and generally greater the older the males were when their maturity was attained.

73 of the 85 females sexually mature at 4 years of age were left the next spring or 86 %. Mortality 14 % has thus been less that year in the females than in the males. Further observations are required, however, to confirm

Table 2. Percentage mortality in perch of different sex and age.

In the year preceding the age of	♂♂			♀♀	Immature
	Early ripe	Medium ripe	Late ripe	Early ripe	
3	27	—	—	—	30
4	18	29	—	—	19
5	29	36	42	14	33

this. The relation between sexual maturity and growth mentioned later should also be noted in this connection.

Mortality in the immature specimens varied as well during different years and lay somewhat above the mortality in the sexually mature specimens. In all the categories mortality was lower during the fourth year, which must, however, depend on outward circumstances.

Relation between Length (Growth) and Sexual Maturity

This question will be dealt with more fully and jointly for several species of fish in a coming paper. We shall now only discuss the present experiments with perch, and first consider the differences between these experiments.

Table 3. Length and frequency of ripe males in groups of two-year-old perch. (A—F=different experiments).

Group	Average length (total) in mm	Number of specimens	Ripe males	
			Number	%
A..................	117	42	16	38
B..................	114	74	32	43
C..................	97	108	4	4
D..................	84	825	90	11
E..................	82	100	12	12
F..................	82	592	77	13

In Table 3 is shown the average size of the two-year-old perch divided among the different experiments as well as the percentage of ripe males. It is apparent from this that in the experiments, where the perch were largest, the percentage of ripe males was rather high (approx. 40 %), while in the experiments with poorer growth and small individual size, on the other hand, the percentage of such males only amounted to 11—13 %. Experiment C with medium growth thus constitutes so far an exception, as the number of males was low there, only 4 %. No clear relation with size could be shown in the experiments with different growth for the males, which first reached sexual maturity at 3 and 4 years of age. It was thus only with smaller size

Table 4. Number of ripe females in experiments with poor and good growing perch.

Age in years	Growth poor			Growth good		
	Number of ripe ♀♀	Per cent ripe ♀♀	Total number of specimens	Number of ripe ♀♀	Per cent ripe ♀♀	Total number of specimens
3	—	—	801	1	—	425
4	—	—	682	85	32	273
5	82	20	402	121	49	247

and lower age (2 years), that individual size affected the commencement of sexual maturity in the males. Mention may be made here that in some experiments started two years later, no males attained sexual maturity even at 2 years of age in one experiment, where the growth was particularly poor (average length 77 mm), while in another experiment with exceedingly good growth 139 specimens out of 260 or 53 %, probably all males, became sexually mature as early as one year of age. Average length was 112 mm for these and 106 mm for those that were not sexually mature.

As far as the females are concerned, there is also a clear relation between sexual maturity and growth. This is evident from table 4. Here a division has been made of the material included in Table 1, so that from and including three years of age the stunted population was kept separate from those with good growth. At three years of age only one sexually mature female could be found. At four years perhaps there were a few sexually mature females in the stunted population, but in the other experiments with a lower total number of fish there were not less than 85 such specimens or 32 %. Fig. 1 shows very clearly this relation between length and sexual maturity, in each experiment separately, for these four-year-old females and not sexually mature specimens (mostly later females). As five-year-olds practically all the females or 49 % were sexually mature among the large fish, but only 20 % in the stunted population. If, as previously mentioned, those not spawning now were females, who would first spawn the next year or later, the sexual ratio in the two populations would be the same or 1/1.

The relation pointed out between better growth and earlier sexual maturity in the different experiments can also be shown in the specimens *within* each experiment. In order to illustrate this, figures for the average length in the different groups of sexual maturity have been placed together in table 5 beginning with the two-year-old males, when sexual maturity first occurred. Mention can first be made that at two years of age in nearly all the experiments the average length of the now sexually mature males was somewhat greater than in the remaining immature specimens in the same experiment, which is shown graphically in fig. 2. The next year, at three years of age, the figures show that the good growth of the males sexually mature the previous year had clearly continued. The average length of these was,

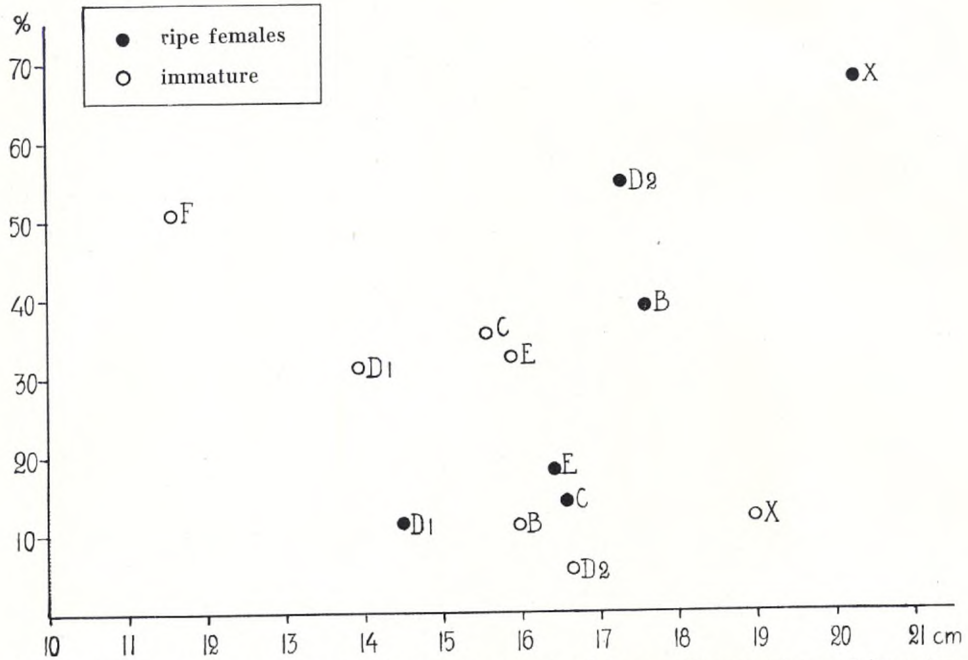

Fig. 1. Relation between mean length and percentage of 4-year-old spawning and immature female perch in different experiments.

namely, still somewhat greater than in the males, which were first now sexually mature. The size of the not yet sexually mature specimens has varied and was sometimes above, sometimes below the size of the smaller males but was still — except in one case — rather less than in the males sexually mature the previous year. At one year more in age (4 years) the relation was different in different experiments. In several of them the average length of the early ripe males was somewhat greater than in the medium ripe. And in every case the good growth in the earliest ripe males continued, in spite of their having spawned year after year. But at the same time the specimens, that were not sexually mature previously, now began to grow better. Many of these had, namely, now developed into sexually mature females, and their average length was throughout — with only one exception (exp. D) greater than in all the other groups. The average length of the specimens, that were still immature, was also greater as a rule than the average length of the males. As the majority of the former consisted of females becoming sexually mature under coming years (cf. above), it is clear that during their fourth year the females began to grow rather faster than the males, and that the now ripe females consisted of the specimens that have grown best (cf. also Fig. 1). This becomes still more obvious during the fifth year. At five years of age both the early ripe females and the new medium females were as a rule considerably larger than the males and even larger than the not yet ripe females occurring in certain experiments.

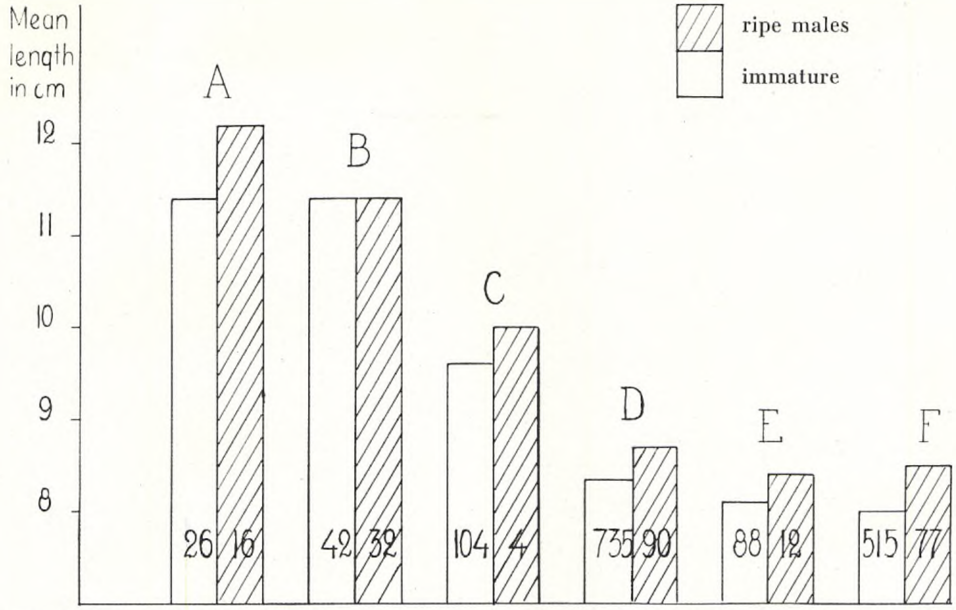

Fig. 2. Mean length in different groups of 2 years old spawning males and immature perch (Numb. of sp. in the columns).

Discussion

The results have shown that in the perch sexual maturity in the females is attained 1 to 2 years later than in the males, that dissimilarities in mortality have occurred in both sexes and in the different groups of sexual maturity, but that the sexual ratio, however, is roughly speaking 1 : 1 year after year. It has also been demonstrated that sexual maturity is dependent on the size of the specimens, and that this is the case both between different populations (different experiments) as between the specimens within each population.

It is a common occurrence in fish that sexual maturity is attained earlier in males than in females. The even sex ratio perhaps appears curious with regard to the results in spawning fishing for perch, when males are often dominant to a great extent (cf. below however). The figures for mortality mentioned, which were higher in the males that became sexually mature later and lowest in the females, seem to indicate that size has been the determining factor. The later males have namely (cf. Table 5) had poorer growth and at the same age all been smaller than the early ripe specimens. And the females on attaining sexual maturity for the first time have been larger than the corresponding males. Mortality during a certain year has thus been greater in the smaller than in the larger specimens. A comparison between the stunted and well-grown populations has also shown that mortality amounted to approx 50 % in the former as opposed to 42 % in the

Table 5. Growth rates (mean length in mm at an age of 2—5 years) of early, medium and late maturing males and females and of immature perch in different groups (experiments).

Sex	Age in years	Groups (Experiment B—F)														
		B			C			D			E			F		
		Early	Medium	Late	Early	Medium	Late	Early	Medium	Late	Early	Medium	Late	Early	Medium	Late
Males	2	114	—	—	100	—	—	87	—	—	84	—	—	85	—	—
	3	153	148	—	130	125	—	110	103	—	117	117	—	110	109	—
	4	165	170	—	150	153	140	147	138	138	155	154	160	115	113	114
	5	182	177	—	—	—	—	183	168	164	—	—	—	137	134	136
Females	4	176	—	—	166	—	—	145	—	—	164	—	—	—	—	—
	5	207	207	—	199	192	—	180	183	—	199	192	—	168	—	—
Immature	2	114			96			83			81			80		
	3	156			127			102			115			108		
	4	160			156			140			159			116		
	5	—			180			180			—			168		

latter case. This appears quite natural. Apart from mortality in natural waters through predatory fish both the intra- and interspecific competition ought, namely, to be more intense in a pond with its limited space than in a lake and, of course, even more intense the larger the population is.

It has been established by several scientists in different connections that in many species of fish a certain relation exists between growth and sexual maturity. The results are, however, not universal. In some species of salmonids and whitefish bad growth seems to be connected with early sexual maturity and a short span of life (FOERSTER 1947, SVÄRDSON 1951). As far as perch is concerned, it has also been established (ALM 1951) that sexual maturity occurs at a lower age in stunted populations than in well-grown populations. In this species as well as in some cyprinids and aquarium fish several scientists (ALM 1946, 1951, LASKAR 1940, OLSTAD 1919, SVÄRDSON 1943) have pointed out that particularly good growth is accompanied by early sexual maturity.

The purpose of these experiments was amongst other things to try in ponds to produce populations with such differences in growth, that they could be considered as corresponding to the well-grown and stunted populations occurring in nature. One should than be able to obtain a definite record of the age when sexual maturity was attained. As has been stated above, it has admittedly been possible through variations in the number of specimens in different ponds to obtain great differences in growth and size of specimens. The earlier sexual maturity, which one could have expected in the most stunted population, has however not occurred. The males in all the experiments have mainly become sexually mature at 3 years of age, and after that at 2 and 4 years, while some were first ripe at 5 years of age, the two-year-old ripe males being more numerous in the experiments with better growth. And it was very clear in the females that sexual maturity occurred later, it is at a greater age, in the stunted than in the well-grown populations. Poor growth and early sexual maturity have thus not been connected in the stunted population, instead the relation has been the opposite. Possibly this depends on the environmental conditions in the experimental ponds being different and undoubtedly much more favourable than in lakes with stunted populations of perch. Growth was also better in the experiment with a stunted population, in spite of being densely stocked, than the figures reported for many lakes with stunted populations of perch (ALM 1946, BROFELDT 1915, RÖPER 1936). The growth in the well-grown populations correspond, on the other hand, with what has been found in well-grown populations of perch in nature (ALM l.c., NILSSON 1921, HILE 1942, OLSTAD 1919).

From these results can thus be established, that both within a certain population as well as when comparing populations with different growth and with an individual size that is above the size of real stunted populations in nature, sexual maturity occurs earlier the better the growth is, and this especially in the females. On account of this latter reason the difference in age for the attainment of sexual maturity in males and females is less the better the growth is in a population.

In the fact that sexual maturity occurs at different ages as well as in the annual losses may be found the reason for spawning fishing in lakes with stunted populations often giving such a high percentage of males. The experiments have shown that at the spawning completed at 5 years of age in the well-grown populations 440 males have taken part in the spawning as opposed to 197 females. The relation between the spawning males and spawning females was thus 69 % and 31 % here. In the stunted populations, however, the corresponding figures are 907 males and only 82 females or 91,7 % resp. 8,3 %. The older a certain year class becomes, the more this contrast will, of course, disappear, as then an ever increasing number of females will become sexually mature. On the other hand the number of specimens in the year class in question decreases more and more. In any case, however, even if a certain year class reaches a great age, the number of males that have managed to take part in spawning must be considerably greater than the number of females. And if the mortality for different reasons becomes very high, perhaps after a few years only, a larger or smaller number of females will never reach the size and age, at which they become ripe.

Summary

An account has been given of the results obtained in certain experiments concerning the time of sexual maturity, mortality, the relation between growth (size) and sexual maturity etc. in perch. The experiments have been carried out in ponds at the Kälarne Fishery Research Station.

Sexual maturity has with normal, comparatively good growth, occurred at 3, and then at 2 and 4 years of age in the males and at 4—6 years in the females.

The sexual ratio has been 1 : 1.

Mortality has been comparatively high, especially the first years. After that it amounted to 20—30 % per annum. It has been higher the later the males became sexually mature and lowest in the females. This implies that mortality has been in inverse correlation to size. Mortality has also, undoubtedly for the same reasons, been somewhat higher in an experiment with a stunted population than in experiments with better growth.

The males have, during the second and partly even during the third year as well, grown better than the females. Later on the conditions have been the opposite.

Sexual maturity has a direct relation to growth. Both in comparison between different experiments as between the specimens in a certain experiment, the specimens with better growth have become sexually mature earlier. The worse the growth has been, the greater has been the difference in time between the attainment of sexual maturity in the males and females. This explains to a great extent why, particularly in stunted populations, the number of males taking part in spawning is far greater than the number of spawning females.

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Studies of the Benthic Fauna in Tributaries of the Kävlinge River, Southern Sweden

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1. Introduction

In 1946—47, the fauna of some streams of the Dee river system in Wales was investigated with reference to seasonal variation, food cycles and as food available for the fish population. The work involved quantitative studies of the lithophilic fauna in two streams, the Ceirw and its tributary, the Merddwr, amplified by general collections from various habitats. The gut contents of many forms were investigated and considered in relation to mode of feeding and to the microscopic planktonic and benthic flora and fauna (Badcock 1949).

Mr. Ph. Wolf of the Swedish Salmon and Trout Association visited these Welsh streams at the sampling stations (Dinmael, near Corwen) shortly before the investigation started and remarked on a superficial resemblance to certain streams in the Kävlinge system of southern Sweden. The Welsh streams were known to be spawning grounds for salmon and as Mr. Wolf hoped to establish salmon in the Kävlinge streams where a natural population of salmon did not occur, he considered that a comparison of the conditions in the two areas might be useful. It was arranged for quantitative samples of the stream bed to be taken by the same method at approximately the same times and for simple routine physical and chemical observations to be made at the times of sampling. Mr. WOLF was responsible for the collection of all the quantitative Swedish samples and routine observations. The author did not visit Sweden until after the end of the sampling period, but worked on the samples preserved in the field and sent from Sweden to the University of Liverpool.

Literature on stream surveys in Britain is cited in BADCOCK 1949. Apparently no general ecological surveys had been made of southern Swedish streams, investigations having been restricted to particular organisms.

In this paper, the Swedish samples will be described; the comparison with the Welsh streams will follow in a further paper.

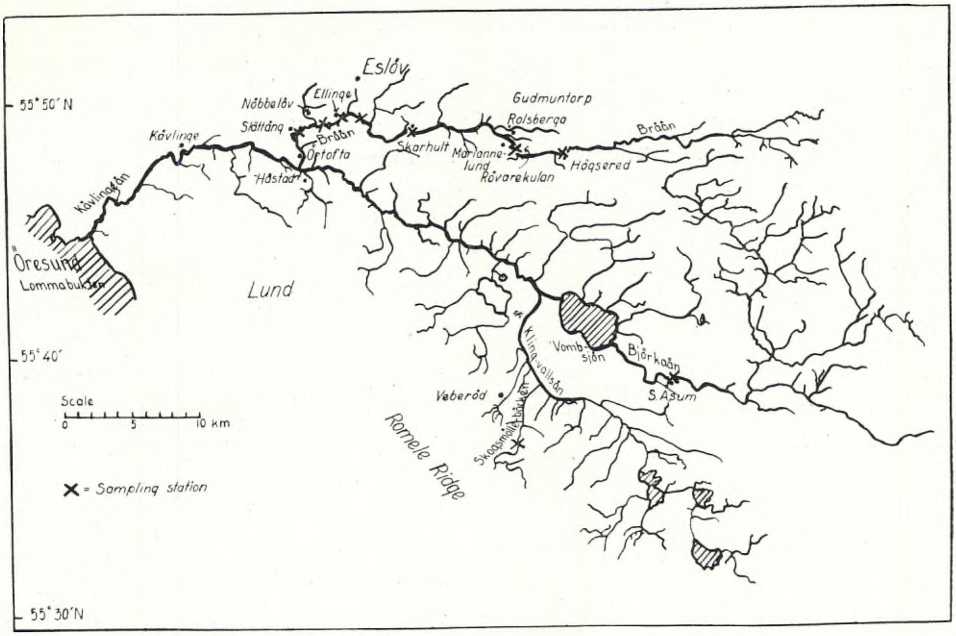
2. Methods

Samples of benthic fauna were collected at fortnightly or monthly intervals in the period September 1946 to July 1947 (with a gap during April and May when no Swedish samples were received). The main streams examined in southern Sweden were the Bråån and Skogsmöllebäcken; a preliminary sample was taken from the Björkaån but subsequently the Bråån was substituted, as sampling in it was more feasible than in the Björkaån. The sampling stations in these streams are shown in Map I. The dates of sampling in the Bråån and Skogsmöllebäcken are given in tables 1 and 2 where the organisms found in each sample are listed.

Each sample consisted of the organisms collected from 2500 sq. cm. of stony stream bed. This area was outlined with a 50×50 sq. cm. frame on the downstream side of which was placed a fine townet in which the organisms collected. Stones were carefully lifted, held in the mouth of the net and rubbed clean. The fine gravel was well stirred up and the flow of the stream washed organisms into the net. Some animals were bound to escape because of the swirl and small forms (below about 3 mm.) were only occasionally retained. Stones and large gravel were removed and the samples preserved in formalin. In the laboratory all the organisms detected by the naked eye were picked out, sieves (ranging down to 0.5 mm.) being used when the sample contained much gravel and silt. The animals were identified and counted.

In order to minimise errors due to local distribution, from April onwards two half samples were taken at a little distance apart and combined.

On each occasion one complete 2500 sq. cm. sample (or two half samples each 50×25 cm.) was collected from the Bråån and a similar one from the



Map. I. The Kävlinge River system showing sampling stations mentioned in this paper.

Skogsmöllebäcken. Care was taken always to move in the same direction for subsequent samples — either up or downstream — so that the same portion of the bed was not resampled. The vegetation was avoided as far as possible so that the quantitative samples represented lithophilic fauna and were comparable.

Physical data recorded included air and water temperatures, depth of water in the measured area and its average surface velocity (roughly estimated by timing a twig as it floated 20 ft. downstream). The oxygen content of the water was determined by the Winkler method (Standard Methods for Water Analysis) and the pH by a suitable indicator.

3. **Environmental Conditions**

Geological and topographical descriptions of the Kävlinge system and an account of its stocking with salmon and sea trout are given by Wolf (1946 and 1950). Some head waters run through moraines rich in limestone which affects the vegetation in the main parts of the river. The Bråån flows mainly over slate formations with some moraine gravel and the water is fairly hard. The quantitative samples were taken in the Gudmuntorp area at Rövarekulan, just south-east of Mariannelund (altitude 89 metres) see Map I, also Wolf 1946 (a) p. 43, sections 420—421 of map of Bråån). The stream

Table 3. Meteorological data for Staffanstorp, Sweden.

Year	Time interval	Rainfall in mm.	Monthly mean of weekly average temp. (air) in °C.	Max. air temp. in °Centigrade.	Min. air temp. in °Centigrade.
1946	1.ix—28.ix	129.6	+13.7	+20.4	+ 5.0
	29.ix—26.x.	21.0	+ 7.0	+17.2	− 8.0
	27.x—30.xi.	42.1	+ 4.0	+ 9.6	− 4.1
	1.xii—28.xii	19.6	− 4.1	+ 7.1	−12.0
1947	29.xii—1.ii.	8.8	− 3.2	+ 5.0	−15.0
	2.ii—1.iii.	7.7	− 7.6	+ 1.5	−16.0
	2.iii—29.iii.	27.3	− 2.7	+ 7.1	−17.0
	30.iii—3.iv.	51.3	+ 5.8	+17.0	− 3.5
	4.iv—31.iv.	12.2	+13.3	+29.0	− 0.5
	1.vi—28.vi.	16.0	+17.1	+31.0	+ 5.8
	29.vi—2.viii.	41.1	+18.1	+35.0	+ 8.3

is some 6—7 metres wide, has a stony slate bed and is moderately stable, with much *Cladophora* and some *Fontinalis*; gravel provides potential spawning ground for salmonids. On one bank, the Bråån is here bordered by a shaley cliff clothed with beech trees (*Fagus sylvatica* L.), but compared with the Skogsmöllebäcken much of the neighbouring land is relatively deforested.

The Skogsmöllebäcken, one of the streams running down the Romele ridge to the Vomb plain, is about 3—4 metres wide at the sampling station (Map I) (altitude 92—94 metres). It is bordered by beech trees and also overshadowed by brushwood (largely brambles, *Rubus fructicosus* L.) and

Table 4. Monthly Rainfall. Lund, Sweden.

Year	Month	Rainfall in mm.	Deviation in mm. of the 1946—47 rainfall from the normal during 1901—1930
1946	ix	121.1	+70.8
	x	20.3	−37.2
	xi	45.7	−12.9
	xii	15.5	−39.3
1947	i	10.5	−34.5
	ii	3.0	−32.7
	iii	47.4	+15.1
	iv	45.3	+ 4.3
	v	10.9	−29.5
	vi	13.9	−32.2
	vii	63.7	− 3.8
	viii	13.6	−62.9
	ix	32.3	−18.0
	x	17.0	−40.5

Table 5. Physical and chemical data for the Bråån (Rövarekulan station) and Skogsmöllebäcken.

	Bråån	Skogsmöllebäcken
Range of average surface velocity of water over measured areas in cm./sec.	24—90	30—70
Range of depth of water in cm. over measured areas	3—65	3—35
Range of water temps. in °C. at times of sampling	0—23	0—24
Range of pH at times of sampling	7.0—8.2	7.5—8.2
$Ca^{\cdot\cdot}$ in mg./l	57.1—71.4	31
Range of dissolved O_2 in mg./l at times of sampling	6.8—14.2	8.0—14.0
The same O_2 range expressed as % saturation of the water with O_2 at stated water temperature	77 (at 22.2° C) to 99 (at 0.2° C)	87 (at 19.2° C) to 97 (at 0.1° C)
Greatest O_2 % saturation recorded at times of sampling	121 % (at 23° C) on 22.vii.47	101 % (at 24° C) on 30.vi.47.
Actual O_2 content in mg./l at greatest saturation	10.4 (22.vii.47)	8.5 (30.vi.47)

herbs such as meadow-sweet (*Spiraea ulmaria* L.), willow herb (*Epilobium sp.*), lesser water parsnip (*Sium erectum* HUDS.) and water mint (*Mentha aquatica* L.). The bed is of gravel with many small emergent boulders. Some of the stones are covered with *Cladophora,* many are bare apart from a rich growth of diatoms. The stream is moderately swift but interrupted by small pools.

These sampling stations are situated about latitude 55° N., longitude 13° E.

Meteorological data for 1946—47, obtained from Staffanstorp (about 20 km. from Skogsmöllan), are given in Table 3. Hours of sunshine were not available. Further rainfall data obtained from Lund (Table 4) indicate that the period October 1946 to October 1947 was, for the most part, unusually dry. The rainfall at Staffanstorp in September 1946 (the commencement of sampling) was high but during the rest of the sampling period it did not exceed a monthly total of 51.3 mm. (April) at Staffanstorp and in February 1947 it was only 7.7 mm.

Physical and chemical data recorded at times of sampling are shown in Table 5. The recorded approximate average surface velocities of the Bråån and Skogsmöllebäcken were often similar but more extreme conditions were recorded in the Bråån at times. The ranges of recorded water temperatures were very similar. The sampling reaches of both the Bråån and the Skogsmöllebäcken were frozen from December 1946 to March 1947 inclusive and for February samples it was necessary to resort to digging; both streams were warm in summer, water temperatures reaching 23 or 24° C. The water was neutral or alkaline, the greater alkalinity (higher pH) occurring on summer days when photosynthesis by the then abundant *Cladophora* would deplete the carbon dioxide content of the water. The pH values are also indicative of calcareous waters. The range of actual calcium content in the Bråån at Mariannelund is calculated from BRINCK 1949; the Skogsmöllebäcken figure comes from the determination of 5.3° hardness Clark (BJÖRKLUND, unpublished). Both streams contain an appreciable amount of calcium but while the water in the Bråån can be described as hard, that in the Skogsmöllebäcken, on the basis of the one determination, is moderately soft. The dissolved oxygen content of the water seems adequate at both stations to support forms intolerant of low oxygen concentrations.

4. **Composition of the Benthic Fauna**

a) *The Bråån.*

i) *Quantitative Samples.*

The organisms found in the quantitative samples from the stony bed at Rövarekulan are listed in Table 1. There was a rich and varied fauna in which insect nymphs and larvae predominated. Dr. P. BRINCK kindly identified the plecopteran nymphs and Mr. R. A. CROWSON the Coleoptera.

The following groups of animals were represented in the samples: —

Oligochaeta.

These were only identified to families; members of the *Naididae, Enchytraeidae, Tubificidae, Lumbriculidae* and *Lumbricidae* were present.

Hirudinea.

Herpobdella and *Pisicola* were identified.

Mollusca.

Ancylastrum fluviatile MÜLLER was the prevalent mollusc; *Planorbis, Pisidium* and *Sphaerium* occurred.

Crustacea.

Gammarus pulex L. was frequent in the samples; one *Astacus* (included in the category 'Miscellaneous') was captured.

Plecopteran nymphs.

Some species of stoneflies are enumerated separately in Table 1. *Leuctra spp.* consisted of *L. hippopus* KEMPNY during the autumn and winter months and *L. fusca* L. (=*L. fusciventris* STEPHENS) in summer. Dr. BRINCK tells

Table 1. Bråån at Rövarekulan: numbers of larger benthic organisms in each sample from 2500 sq. cm. of stony stream bed.

Day and month	1946				1947					
	30.x	7.xi	27.xi	19.xii	2.ii	20.ii	20.iii	17.vi	28.vi	22.vii
Oligochaeta										
Naididae	—	—	—	—	6	—	—	2	—	2
Enchytraeidae + Tubificidae	—	—	56	—	—	—	—	—	1	—
Lumbriculidae	—	—	—	—	—	—	—	—	3	—
Lumbricidae	—	1	—	—	—	—	—	—	—	—
Hirudinea										
Herpobdella	—	—	—	—	—	—	1	—	4	—
Pisicola	1	—	—	—	—	—	—	—	—	—
Indetermined	—	—	—	1	—	—	—	—	—	5
Mollusca										
**Ancylastrum fluviatile* (MÜLLER)	18	34	2	27	32	2	20	8	28	67
Planorbis	—	1	—	—	—	—	—	—	—	—
Pisidium	—	—	—	—	—	—	1	—	—	2
Sphaerium	—	2	4	2	—	—	—	—	—	—
Crustacea										
**Gammarus pulex* L.	2	—	10	—	—	2	—	217	3	26
Plecopteran nymphs										
Isoperla grammatica (PODA)	1	—	2	10	1	9	—	—	1	—
Isoperla diffiformis (KLAPÁLEK)	—	—	—	—	—	—	—	—	—	1
Capnia bifrons (NEWMAN)	—	—	—	—	2	1	—	—	—	—
**Leuctra* spp.	2	1	—	1	1	—	—	25	77	51
Protonemura meyeri (PICTET)	—	—	—	2	—	—	—	—	—	—
Amphinemura sulcicollis STEPH.) (=*cinerea* (OLIIVER))	—	—	—	—	1	4	—	—	—	—
Nemoura spp.	2	—	—	—	—	—	—	—	—	—
Indetermined (damaged etc.)	4	—	—	—	8	—	1	—	—	—
Ephemeropteran nymphs										
*Baëtids	47	108	166	18	215	33	12	142	889	216
**Ephemerella*	—	—	—	—	—	—	—	153	90	39
Ecdyonurus	7	3	1	4	15	2	2	5	—	12
Caenis	10	18	22	18	9	—	3	—	—	21
Ephemera	—	—	—	—	1	—	—	—	—	3
Trichoptera										
Rhyacophila pupae	—	—	—	2	1	1	—	13	10	1
Rhyacophila larvae	—	—	—	—	—	—	—	4	10	4
**Hydroptila* larvae	8	14	5	9	—	—	—	20	4	8
**Hydroptila* pupae	—	—	—	—	—	—	—	16	4	20
Chimarrha marginata L. larvae	—	—	—	—	—	—	—	—	102	—
Polycentropus larvae	17	8	1	5	1	1	—	10	4	15
Polycentropus pupae	—	—	—	—	—	—	—	1	—	—
Psychomyia pusilla F. larvae	—	—	—	17	1	—	1	2	—	5
**Hydropsyche* spp. larvae	47	49	5	25	6	1	5	1	365	126
Hydropsyche spp. pupae	—	—	—	—	—	—	—	1	15	—
Limnophilid larvae	—	—	—	—	—	—	—	1	—	—
Leptocerid larvae	5	—	—	1	1	—	1	—	8	2
Leptocerid pupae (*Mystacides*)	—	—	—	—	—	—	—	—	1	—
Goerinae larvae	3	8	—	1	1	1	—	1	7	—
Goerinae pupae	1	5	—	1	—	1	—	2	1	1
Sericostoma personatum SPENCE larvae	—	32	7	1	—	—	—	—	—	—
Indetermined larvules	6	—	—	—	—	1	—	—	—	—

Table 1 (continued).

Day and month	1946				1947					
	30.x	7.xi	27.xi	19.xii	2.ii	20.ii	20.iii	17.vi	28.vi	22.vii
Coleoptera										
Orectochilus villosus (MUELLER) larvae	—	3	1	4	—	—	1	—	—	3
Hydraena gracilis GERMAR imagines	—	—	—	—	—	—	—	—	3	4
Helodid larvae	—	—	—	—	—	—	—	1	—	—
Elmis maugei BEDEL imagines	—	—	—	—	1	—	—	6	5	6
Elmis sp (?*maugei*) larvae	1	3	—	2	—	—	5	—	1	2
Limnius tuberculatus MUELLER imagines	—	2	—	—	—	—	1	—	—	—
Limnius larvae	3	5	—	6	—	—	2	—	1	29
Diptera										
*Chironomid larvae	164	84	12	253	24	10	147	443	1184	643
Simulium larvae	—	—	—	—	—	—	—	5	21	—
Dicranota larvae (*Tipulidae*)	1	1	—	—	—	—	—	4	18	7
Other tipulid larvae	1	2	—	—	3	—	—	—	1	13
Other dipteran larvae	—	—	—	—	—	—	—	—	—	2
Dipteran pupae	—	—	—	—	—	—	1	—	31	20
Miscellaneous	—	1	2	—	1	—	—	2	4	3
Total number of organisms per sample	351	385	296	410	331	69	204	1085	2896	1359

me that *Capnia bifrons* NEWMAN normally dwells in adjacent cold trickles but occurs in the Bråån during the winter.

Ephemeropteran nymphs.

Apart from the *Baëtidae*, the genera of *Ephemeroptera* recorded in the samples are all listed in Table 1. Specific identifications were not made. The majority of the Baëtid nymphs were *Baëtis spp.* but *Centroptilum* occurred.

Trichoptera.

A wide range of caddis fly larvae are listed in Table 1, but species of *Hydropsyche* (*H. pellucidula* CURTIS, *H. angustipennis* CURTIS and *H. instabilis* CURTIS) predominated. Polycentropids were mainly *Polycentropus* but *Plectrocnemia* also occurred. *Goerinae* included both *Goera* and *Silo*. The Ichneumonoid *Agriotypus armatus* CURTIS, with its characteristic respiratory filament projecting from the stony caddis case (FISHER 1932), was often found as a parasite in *Goerinae* pupae. Apart from the *Goerinae*, the occurrence of Trichopteran pupae was confined to the summer months. Presumably in the few *Goerinae* pupae recorded during the winter, parasitisation had prevented metamorphosis.

Coleoptera.

The species of *Coleoptera* are all listed in Table 1. Elmids and the gyrinid *Orectochilus villosus* (MUELLER) predominated.

Diptera.

Apart from the abundant chironomids (=tendipedids), dipteran larvae were represented by *Simulium* (not very common in the samples), tipulids of which *Dicranota* was the most prevalent, and a few rarer forms such as *Atherix* and *Tabanus* which are included in the category 'other dipteran larvae'. Dipteran pupae were mainly chironomids, with some *Simulium.*

Miscellaneous.

The term 'Miscellaneous' comprises animals very rarely recorded in the samples e.g. salmon fry (*Salmo salar* L.), a minnow (*Phoxinus phoxinus* (L.)), and the one crayfish (*Astacus*), also adventitious forms.

The sampling was not entirely comprehensive of the lithophilic fauna. As previously stated, some animals would escape sampling and organisms less than about 3 mm. in length were only occasionally retained. Also, delicate organisms such as *Turbellaria* would be damaged during transit from Sweden in a mixed sample containing gravel. *Turbellaria* were virtually absent from the samples received but on visiting Sweden, *Dendrocoelum lacteum* (MÜLLER) was found in the Bråån.

Specific identification of nymphs and larvae in Swedish samples was not feasible in many instances. The material had to be preserved before transit to England and in preserved material it is not always possible to make out the necessary diagnostic characters, also breeding out of those insect nymphs and larvae for which suitable keys were not available was precluded. It was not possible to attempt breeding out during the short (two weeks) subsequent visit to Sweden in August 1949.

ii) *General Collections.*

General collections made during the brief visit in August 1949 showed that, in most respects, the rich and varied population indicated by the samples was qualitatively typical of the Bråån for its upper reaches in the Högseröd and Gudmuntorp districts, above the entry of pollution from a dairy at Rölsberga.

The various collecting stations are shown on Map I. At Skarhult, downstream from Rölsberga, the river had a predominantly sandy bed interspersed with some large stones supporting much *Spongilla lacustris* (L.) and *Cladophora. Polycentropus* larvae were frequent here; *Herpobdella* and *Asellus* also sheltered under the stones. These forms are tolerant of more eutrophic conditions and can withstand slight pollution. Some portions of the river in this area had a rather swifter flow with a more stony bed on which *Fontinalis* occurred.

Lower down at the Damstorp bridge, the river no longer has the appearance of an upland trout brook and is bordered by *Sparganium erectum* L. *Polycentropus* and various other caddis were common but *Hydropsyche,* prevalent in the unpolluted upland reach, was absent here. Below this point, sewage from Eslöv enters the river; some is treated first in sewage ponds but these are inadequate and at peak times a certain amount of crude sewage enters the river directly.

Downstream at Ellinge, the river has a stony bed and is muddy and rather dirty from pollution. Patches of *Glyceria* occur. The leech *Herpobdella* is common; chironomid larvae and, in places, some *Baëtis* nymphs and *Simulium* larvae were collected. These latter forms indicate recovery from pollution to some extent — or possibly that these points had escaped the main force of the pollution current. Near the Nöbbelöv road, the water was still slightly muddy. Leeches, especially *Herpobdella,* were frequent; *Cladophora* grew on some stones and there appeared to be a considerable amount of algal slime. Near Slättäng, the water was clear and there were no obvious signs of pollution; conspicuous plant growth consisted of *Myriophyllum* and *Cladcphora*; Among the stones, *Hydropsyche* larvae were frequent. South of this at Örtofta, the Bråån has become a muddy river of the lowland water course type; it enters the Kävlinge river at Håstad, just south of Örtofta village.

These samples and cursory collections serve to indicate that the benthic fauna of the Bråån is intrinsically rich and consists of a wide variety of organisms except where affected by pollution. If this were controlled, it should be able to support a numerous fish population.

b) *The Björkaån.*

The single sample collected from the Björkaån near S. Åsum on 10.ix.46 may be of interest in indicating that it too has a rich and varied bottom fauna. The animals obtained from 2500 sq. cm. of stony stream bed are listed below.

Hirudinea	
Glossosiphonia complanata	2
Herpobdella octoculata	45
Mollusca	
Ancylastrum	120
Valvata	2
Bithynia	8
Crustacea	
Gammarus pulex L.	54
Plecopteran nymphs	
Chloroperla burmeisteri (PICTET)	1
Leuctra hippopus KEMPNY	2
Taeniopteryx nebulosa (L.)	1
Indetermined	3

Ephemeropteran nymphs	
Baëtis spp.	67
Ephemerella	1
Ecdyonurus	7
Hemiptera	
Aphelocheirus	9
Trichoptera	
Rhyacophila larvae	3
Rhyacophila pupa	1
Hydroptila larvae	23
Hydropsyche larvae	569
Polycentropus larvae	15

Coleoptera	
Limnius imagines	3
Elmid larvae	105
Haliplid larva	1

Diptera	
Chironomid larvae	218
Chironomid pupae	2
Simulium larvae	2
Tipulid larvae	2
Tabanus larvae	4

Total number of organisms in sample=1270.

c) *The Skogsmöllebäcken.*

Animals found in the quantitative samples from the Skogsmöllebäcken are listed in table 2, the following groups being represented: —

Oligochaeta.

Naidids, enchytraeids, tubificids and lumbricids occurred.

Mollusca.

Ancylastrum fluviatile was prevalent, *Planorbis, Bithynia* and *Pisidium* occurred.

Crustacea.

Gammarus pulex was present in all samples and generally abundant.

Plecopteran nymphs.

Leuctra spp., as in the Bråån, comprised *L. hippopus* during the autumn and winter months and *L. fusca* in summer. The species of *Nemoura* were *N. erratica* CLAASEN and *N. cinerea* RETZIUS (=*N. variegata* PICTET). *Capnia bifrons, Brachyptera risi* (MORTON) and *Taeniopteryx nebulosa* occurred.

Baëtid nymphs, the prevalent ephemeropterans, again consisted almost exclusively of *Baëtis* spp. but *Centroptilum* was recorded. Other Ephemeroptera were *Ephemerella, Ecdyonurus, Caenis* and *Ephemera.*

Trichoptera.

A wide range of caddis larvae and pupae are listed in table 2. As in the Bråån, goerinid caddis pupae were frequently parasitised by *Agriotypus armatus.*

Coleoptera.

These are listed in table 2. *Elmidae* and *Hydraena gracilis* were the most frequent of the *Coleoptera.* 'Elmid imagines' included *Elmis latreillei* BEDEL.

Diptera.

Again the chironomid larvae predominated, *Simulium* larvae occurred and *Dicranota* was the most frequent of the tipulids.

Miscellaneous.

This term included adventitious forms and occasionally a young fish.

Table 2. Skogsmöllebäcken: numbers of larger benthic organisms in each sample from 2500 sq. cm. of stony stream bed.

Day and month	1946						1947				
	10.ix	8.x	30.x	7.xi	25.xi	20.xii	1.ii	20.ii	20.iii	18.vi	30.vi
Oligochaeta											
Naididae	—	—	—	3	2	—	—	—	—	3	—
Enchytraeidae & Tubificidae	—	3	—	—	—	—	—	5	—	—	—
Lumbricidae	—	1	—	1	1	—	—	—	—	1	—
Indetermined	—	1	—	—	—	—	—	—	—	—	—
Mollusca											
**Ancylastrum fluviatile* (MÜLLER)	69	66	9	29	48	28	30	7	10	4	3
Planorbis	1	—	—	—	—	—	—	—	—	—	—
Bithynia	—	—	—	—	—	—	—	1	—	—	—
Pisidium	1	—	—	—	—	—	—	—	—	—	7
Crustacea											
**Gammarus pulex* L.	73	76	47	116	149	21	50	16	57	2	913
Plecopteran nymphs											
Brachyptera risi (MORTON)	—	—	—	1	9	5	—	—	3	—	—
Taeniopteryx nebulosa (L.)	1	—	—	—	—	—	—	—	—	—	—
Capnia bifrons (NEWMAN)	—	—	4	—	46	—	17	—	16	—	—
**Leuctra* spp.	25	18	23	52	43	19	10	—	32	37	—
**Nemoura* spp.	11	5	2	19	14	4	33	—	36	—	—
Indetermined (damaged etc.)	—	3	—	2	—	1	—	—	—	—	—
Ephemeropteran nymphs											
*Baëtids	23	35	138	214	227	114	377	—	137	483	—
**Ephemerella*	5	—	—	—	—	—	—	—	—	190	80
**Ecdyonurus*	2	7	16	18	33	14	30	1	2	—	—
Caenis	—	—	—	—	—	2	2	—	—	4	—
Ephemera	—	1	—	1	1	—	—	8	—	—	1
Trichoptera											
Rhyacophila larvae	—	—	—	—	1	2	8	—	1	4	—
Rhyacophila pupa	1	—	—	—	—	—	—	—	—	—	—
Hydroptila larva	1	—	—	—	1	—	—	—	—	—	—
Hydroptila pupae	—	—	—	—	—	—	—	—	—	4	3
Chimarrha marginata L. larvae	1	—	—	—	—	—	—	—	—	10	—
Polycentropus larvae	139	23	6	14	9	6	1	3	—	2	3
Polycentropus pupae	—	—	—	—	—	—	—	—	—	—	4
Psychomyia pusilla F. larvae	7	9	—	—	5	1	5	10	—	26	—
Hydropsyche spp. larvae	12	8	3	8	11	18	7	1	2	8	—
Limnophilid larvae	1	—	—	—	—	—	—	1	—	—	1
Limnophilid pupa	1	—	—	—	—	—	—	—	—	—	—
Mystacides larvae	—	—	—	—	—	—	—	—	—	2	—
Goerinae larvae	3	1	—	4	6	2	—	2	—	1	—
Goerinae pupae	6	8	2	2	—	1	1	—	7	4	—
Sericostoma personatum SPENCE larvae	—	—	—	2	—	—	—	—	—	—	—
Indetermined larvules	—	—	11	1	—	—	—	—	—	—	—
Indetermined pupae	2	—	—	—	—	—	—	—	—	—	—
Coleoptera											
Haliplid imagine	—	—	—	—	1	—	—	—	—	—	—
Hydraena gracilis GERMAR imagines	—	—	—	3	—	—	3	—	2	—	—
Helodid larva	—	1	—	—	—	—	—	—	—	—	—
Elmid imagines	—	—	—	1	3	1	1	—	—	1	—
Elmid larvae	3	2	—	—	1	3	3	4	1	1	3
Latelmis (?*volkmari*) larvae	1	—	2	2	3	—	—	—	1	—	1
Indetermined imagines (lost)	—	—	—	—	—	—	—	—	—	3	—

Table 2 (continued).

Day and month	1946						1947				
	10.ix	8.x	30.x	7.xi	25.xi	20.xii	1.ii	20.ii	20.iii	18.vi	30.vi
Diptera											
*Chironomid larvae	132	6	13	18	35	28	59	85	22	896	6
Simulium larvae	—	—	—	9	6	11	7	—	—	3	—
Dicranota larvae (*Tipulidae*)	—	3	1	1	4	—	2	—	—	4	—
Other tipulid larvae	1	1	1	2	—	—	—	—	1	—	—
Other dipteran larvae	—	—	—	2	—	—	—	—	—	—	—
Dipteran pupae	7	—	—	—	—	—	—	—	—	1	—
Miscellaneous	1	—	3	1	—	1	—	—	1	2	—
Total number of organisms per sample	530	278	281	526	659	282	646	114	331	1697	1025

General collections in the Skogsmöllebäcken gave a similar qualitative picture to the quantitative samples.

5. **Discussion**

In discussing the Welsh samples (BADCOCK 1949), the need for extreme caution in interpreting the quantitative data was stressed. Firstly, there are errors due to sampling method, some organisms being swirled out of the net and lost, especially during spates. Experiments with an outer net to trap escaping animals showed a loss ranging from 4 to 20 % of the total fauna retained in both nets (3.7 to 24 % of fauna retained in inner net). Secondly, and more important, is the great variability of a stony stream bed which offers numerous different microhabitats. There may be many kinds of these habitats within even a small portion of stream. They are partly determined by the speed of the current, which is dependent primarily on rainfall, slope and type of land, but often varies greatly locally according to the kind, size and shape of the stones over or round which the water is flowing. The microhabitats are also determined by whether or not the stones have sheltered crevices, are fixed or loose and whether there is a localised accumulation of sand, silt or débris, a tuft of moss or a particularly dense clump of algal filaments or well established growth of diatoms. These microhabitats may or may not chance to be colonised and the clusters of organisms may or may not be included in a sample. The irregularity of distribution may be demonstrated by a comparison of two half samples collected in the Bråån (Table 6).

The total number of organisms in the whole sample becomes 1359, whereas if A had been repeated, the total would have been 1924, or if B had, then it would have been 794. Hence the point of collecting two half samples a little

Table 6. Quantitative yield of two half samples from the Bråån. 27.vii.47.

	Half sample A.	Half sample B.
Chironomid larvae	397	246
Other forms	565	151
Total numbers of organisms	962	397

distance apart in an effort to minimise errors due to local distribution. This example emphasises the necessity of taking a large number of samples if adequate statistics on the fauna are to be obtained and that only broad generalisations should be made from the numerical data.

Although the actual numbers must be treated with great caution, certain statements can be derived from Tables 1 and 2.

Most of the categories of organisms are not represented in any of the samples (except perhaps one) by numbers greater than 25 (i.e. 25 individuals per 2500 sq. cm.). The forms represented by population density greater than 25 in more than one sample are marked * in Tables 1 and 2.

In both the Bråån and the Skogsmöllebäcken, *Leuctra spp.,* Baëtid and *Ephemerella* nymphs, chironomid larvae, *Ancylastrum fluviatile* and *Gammarus pulex* all come into the starred category of 'over 25 individuals per 2500 sq. cm. in more than one sample'. *Hydropsyche* larvae and *Hydroptila* (if lavae and pupae are considered together) come into the 'over 25' group only in the Bråån and not in the Skogsmöllebäcken, while *Nemoura* and *Ecdyonurus* nymphs are in the 'over 25' category only in the Skogsmöllebäcken. *Nemoura* and *Ecdyonurus* were not as numerous as other members of this 'abundant' category.

Organisms which were less abundant but had a density of over 15 (i.e. between 15 and 25 individuals per 2500 sq. cm.) in more than one sample were *Caenis* and *Polycentropus* in the Bråån, *Capnia bifrons, Hydropsyche* and *Polycentropus* in the Skogsmöllebäcken. One particularly large assembly of *Chimarrha marginata* larvae occurred in a Bråån sample but they were not regularly abundant. *Sericostoma personatum* and *Limnius* larvae were also quite numerous in one Bråån sample. Other forms were less numerous.

The population density of the intermediate and less numerous forms is generally very markedly lower than that of the 'over 25' category and the usual range of variation much more restricted (0—25); in contrast the chironomid larvae might reach several hundred or even over a thousand in one sample.

In the single sample from the Björkaån, the most numerous forms include some of those already discussed: — *Ancylastrum fluviatile, Gammarus pulex,* Baëtid nymphs, *Hydropsyche,* elmid and chironomid larvae. In addition in this sample there were many young leeches of the genus *Herpobdella.*

It is noteworthy that the majority of the more abundant organisms are phytophagous and/or detritus feeders (*Leuctra, Nemoura,* Baëtids, *Ephemerella* and *Ecdyonurus* nymphs, *Ancylastrum, Gammarus pulex* and the chironomid larvae except for the tanypodinid fraction), while *Hydropsyche* is omnivorous. Predominantly carnivorous forms are generally less numerous.

As in the Welsh samples, the figures for some of the less numerous forms may indicate a seasonal distribution but the number of samples is too few to establish this for any form, while loss of the smaller individuals from the sampling apparatus leaves open the question of whether seasonal absence from the samples is due to small size or to actual absence from the site.

It is however interesting to compare the range of the total number of organisms per sample between September 1946 and March 1947 inclusive with that during summer (June and July 1947) (Table 7).

Table 7. Range of total number of organisms per sample from 2500 sq. cm. of stony stream bed.

Season	Bråån	Skogsmöllebäcken
September to March	69—410	144—659
June and July	1085—2896	1025 and 1697 (two samples only)

Despite the great variability, this serves to stress the larger population of the stone fauna in the summer months compared with the winter. Seasonal averages (Table 8) are also illuminating.

Table 8. Seasonal averages for total number of organisms collected from 2500 sq. cm. of stony stream bed.

Period	Bråån Average	Skogsmöllebäcken Average
Autumn 1946 (Sept., Oct. and Nov.)	344 Av. of 3 samples	455 Av. of 5 samples
Winter 1946—47 (Dec., Feb., March)	251 Av. of 4 samples	351 Av. of 4 samples
Summer 1947 (June and July)	1780 Av. of 3 samples	1361 Av. of 2 samples

Owing to variation, the actual numbers have little meaning but the differences between winter and summer samples are significant. The summer increase is due mainly to insect nymphs and larvae.

Seasonal variation in the Welsh samples is discussed in the previous paper (BADCOCK 1949), where the possibility of migration of organisms from the bare stones to more sheltered sites, such as moss, during winter is suggested. Further observations in streams near Glasgow (BADCOCK, unpublished) indicate that some organisms may burrow down into the gravel during winter. The inclusion of leaves and *Cladophora* in some Swedish samples during winter and the fact that digging was necessary at times in icy weather may indicate that some sheltered microhabitats were included and so more animals were recorded than might otherwise have been the case.

As in the Welsh streams, certain groups of organisms predominated in the fauna of these Swedish streams. On expressing various groups of organisms as percentages of the total population collected quantitatively between September 1946 and July 1947 inclusive, over three quarters of the fauna collected was composed of three groups of organisms, two of which were common to both streams, but the third group differed (Table 9).

Table 9. Percentage of total population.

	Bråån	Skogsmöllebäcken
Chironomid larvae	40	20
Ephemeropteran nymphs	31	34
Gammarus pulex	(4)	24
Trichoptera	14	(6)
Sum of the three groups	85	78

As has been shown by many workers (see references — Hynes 1950) the insect nymphs and larvae are important as food for salmon and trout, but Allen (1941) showed that *Gammarus* has a low availability factor for salmon parr.

The quantitative samples from the Bråån and Skogsmöllebäcken can probably be regarded as indicating the minimum productivity at the sampling stations, for apart from loss during sampling, the lithophilic fauna is known to be less rich than that of vegetation such as mosses and *Cladophora* (Percival and Whitehead 1929). The unavoidable inclusion of some *Cladophora* would increase the numbers of some animals in the Swedish samples.

The comparison of the samples from the Welsh Ceirw and Merddwr with those from the Swedish Bråån and Skogsmöllebäcken will be discussed in a further paper.

6. Summary

Seasonal quantitative samples of the fauna from the stony bed of two Swedish streams, the Bråån and the Skogsmöllebäcken have been identified as far as possible and are described and discussed. The fauna at the sampling stations was rich and varied, with insect nymphs and larvae predominating.

If the quantitative samples are adequately representative of the Bråån and Skogsmöllebäcken, and temperature is disregarded, there seems no fundamental biological reason why these streams could not support a thriving salmonid population, provided pollution were controlled, fish passes provided round mechanical barriers and adequate legislation introduced to ensure the welfare of the salmonids throughout all phases of the life history.

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Comparative Studies in the Populations of Streams

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Many criticisms can be — and have been — directed at both the qualitative and quantitative aspects of studies in stream populations, but it is easier to be destructive than constructive, and our fundamental knowledge of these communities and the factors involved in the qualitative and quantitative differences in them is still often very inadequate.

Firstly, a brief mention will be made of some existing qualitative classifications of streams. THIENEMANN's (1912) scheme, based largely on fish zones, was adapted and extended by CARPENTER (1928) for running waters in Britain and is still useful as far as it goes. She broadly divides reaches of running waters into (1) headstreams and highland brooks, (2) the trout beck, (3) the minnow reach (i.e. Grayling zone — Die Äschenregion — of THIENEMANN), (4) the lowland course, (5) the brackish estuary. It is clear that this does not take into account the frequent local variations within a so-called homogeneous reach, or the differences in the invertebrate fauna of ostensibly the same reach in different rivers on diverse geological formations. For instance, communities in a calcareous trout beck may differ greatly in species and density from those in a soft water trout beck.

RICKER's (1934) classification of running waters in Ontario is based on the volume of water in Cu. ft./sec. flowing on June 1st, on the maximum summer temperature (over or under 24° C) and on slow or swift, hard or soft waters. It suffers from being too arbitrary — a stream is not uniform in space or time — and does not succeed in providing a natural classification in which certain physical and chemical features with associated dominant organisms, can be clearly discerned.

PEARSE (1926) and HORA (1930) both classify organisms in running waters according to their habitats, basing their primary divisions on current relations and habit of life. HORA, who modified and extended PEARSE's scheme, recognises in rapidly flowing streams four main animal associations — namely, animals of pools and sides of streams, burrowers, swimmers, and swift-current inhabitants. He further deals with sub-associations (plant or rock dwellers) and finally with strata such as root-inhabiting animals, animals on exposed rock surfaces, on the under side of rocks, among pebbles and shingle, etc. This is not altogether satisfactory as in practice there are no hard and fast lines between these divisions, and animals may be found in more than one habitat — in fact, there may be seasonal migration from one habitat to another.

HYNES (1941), in his study of the ecology of stone fly nymphs, pointed out that it was impossible at that time to produce a detailed classification which was infallible because the actual factors controlling the distribution of many aquatic animals were quite unknown. Therefore, he classifies stone fly habitats only on obvious physiographical data.

BERG (1948), in discussing the extensive survey of the Susaa system, depicts eleven biotopes in it, all of which — except for the estuarine one — are delimited by the prevailing velocity of the current and the substratum. He mentions some of the other factors involved in distribution; these would need to be incorporated in a scheme of more universal application.

Possibly in the future some satisfactory combination of the various classifications may be found feasible and be able to take into account physiographical features including temperature range, also chemical factors and habitat range, with associated communities. However, much work is needed first.

Where quantitative studies are concerned, criticisms can be levelled at the inaccuracies due to methods of sampling and of dealing with the catch, and at the unreliability of the samples owing to the great variation in — for example — a stony stream bed with its many microhabitats — until at times one begins to wonder if there is any value left in quantitative work in streams.

My own samples from tributary streams of the Dee (BADCOCK 1949) and from certain streams in southern Sweden (BADCOCK 1954) showed considerable variation in adjacent samples, while MOTTLEY, RAYNOR and RAINWATER (1938) cast grave doubt on the significance of the numbers of organisms in quantitative samples, by finding — as a result of large numbers of samples — that the distribution of aquatic insects in a stream was not random but definitely bunched. LEONARD (1939) also showed variation in the composition of samples but found that the *total volume* of organisms present in a given area was more consistent.

As well as variation within the one major habitat such as bare stones, there may also be variation in the nature and density of the fauna in diverse although possibly adjacent habitats, a feature emphasized by the pioneer work of PERCIVAL and WHITEHEAD (1929).

Seasonal variation, too, may be considerable — a feature sometimes conveniently ignored by workers who omit to state the season of their sampling,

Table 1. Seasonal averages for total number of organisms collected from 2500 sq. cm. of stony stream bed.

	Ceirw A & B		Merddwr A	
	Average	No. of samples averaged	Average	No. of samples averaged
Autumn 1946 (September and October	50	(8)	63	(4)
Winter 1946—7 (December and January)	38	(3)	26	(2)
Spring 1947 (April and May	204	(3)	215	(2)
Summer 1947 (June and July)	415	(6)	289	(3)
	Bråån		Skogsmöllebäcken	
Autumn 1946 (September, October and November)	344	(3)	455	(5)
Winter 1947 (December, February, March)	251	(4)	351	(4)
Summer 1947 (June and July)	1780	(3)	1361	(2)

or who lump samples together or average them without paying due attention to seasonal variation and saying clearly what they are doing.

In the Ceirw and the Merddwr, tributaries of the Welsh Dee, despite the variation in the numbers of organisms in a sample, there was a marked statistically significant difference between the numbers per sample from 2500 sq. cm. of stony stream bed in winter and in summer. The average (for Ceirw and Merddwr samples combined) in December and January samples was 33 organisms (average of 5 samples), while the average in June and July was 373 (average of 9 samples).

The same trend was found at all three of the Welsh stations and in samples taken by the same method in streams in southern Sweden (Table 1). In the paper on the Welsh streams it was pointed out that in interpreting the winter minimum, the slow growth, small size and hence potential escape of many nymphs and larvae at that time should be remembered, but the possibility of migrations was suggested. Migrations from the bare stones to more sheltered habitats such as moss might occur in response to some stimulus or as a result of floods and then there might be a recolonisation in spring from the sheltered nidus. The suggestion is supported by WHITEHEAD's (1935) results in the Driffield chalk stream and by the fact that FROST (1942) found a winter peak of chironomid larvae in her moss samples from the Liffey. My own further investigations in streams near Glasgow have strengthened my belief in migrations from the superficial bare stones, for they showed that many nymphs and larvae may burrow down into the gravel during winter to a depth of some 12 cms. and might be missed by normal sampling.

Obviously only very general conclusions can be drawn from the actual numbers of organisms in a sample and even broad generalisations are useless unless habitat, sampling method and seasons of sampling are stated.

Grading of streams, such as has been advocated by certain American Fishery workers, is of very doubtful value — e.g. application of MADSEN's (1935) numerical standards for Arizona streams. He classified streams as *rich* if they had more than 2152 bottom organisms per sq. metre, *average* if between 1076 and 2152 and *poor* with less than 1076. HAZZARD (1935) has given similar standards using weights.

Nevertheless, where methods and seasons are comparable, certain conclusions can be drawn from a study of the numbers of organisms in quantitative samples. The first table showed that irrespective of the actual numbers, the Swedish samples were consistently richer than the Welsh in total numbers of organisms. Table 2 shows the ranges of numbers of organisms in the samples and emphasizes this point.

Table 2. Range of total number of organisms per sample from 2500 sq. cm. of stony stream bed.

	Ceirw (A & B)	Merddwr	Bråån	Skogsmöllebäcken
September to March	10 to 122	10 to 94	96 to 410	144 to 659
June and July	175 to 924	166 to 372	1085 to 2896	1025 to 1697

Provided enough samples are taken, the quantitative method of stream sampling enables the relative abundance of the various organisms to be fairly estimated, preventing on the one hand the overstressing of some which, though larger and more conspicuous, are not really numerous, and on the other hand the overlooking of some of the rarer forms which in more haphazard qualitative collecting might well be missed. So it is helpful in assessing dominants and in depicting the structure of the whole community. In comparing the benthic populations of different streams or reaches of streams, often the difference is not so much qualitative as quantitative — many of the same organisms may be present but the emphasis may shift; the dominants may differ and so may the population density.

Despite imperfections, I consider that quantitative surveys are of some general value in giving a picture of streams and in providing a basis for further investigation. They can well lead on to a study of differences between faunas and an analysis of the causal factors. This analysis may involve special studies of individual species and necessitate experimental work before it can begin to be conclusive.

The point may be illustrated by reference to the samples of benthic fauna taken at approximately the same times from streams in North Wales and Southern Sweden. As already shown, the total population density in the Swedish samples was greater than in the Welsh.

Table 3. Various groups as percentages of the total fauna.

(Based on all the quantitative samples collected at the stations between September 1946 and July 1947.)

	Ceirw A & B	Merddwr A	Bråån	Skogsmöllebäcken
Chironomid larvae	48	25	40	20
Ephemeropteran nymphs	15	23	31	34
Trichopteran larvae and pupae	10	21	14	(6)
Plecopteran nymphs	16	8	(3)	(8)
Gammarus pulex	(1)	(5)	(4)	24
Sum of percentages of predominant groups	89	77	85	78

Certain organisms differed in the various streams, as did the relative importance of some groups of organisms. Table 3 shows the percentage of predominant organisms composing over three-quarters of the fauna in the samples. Chironomid larvae and ephemeropteran nymphs were important in all a four streams. Stone fly nymphs were relatively less important in the Swedish Bråån than in the Welsh Ceirw and Merddwr. *Gammarus pulex* while occurring at all stations was only predominant in the Skogsmöllebäcken and caddises were relatively less important in the latter than in the other streams.

An attempt will be made to summarise the factors probably involved in the differential qualitative and quantitative distribution.

The geographical location of the streams is important in two main ways — in the purely spatial aspect, for example, whether or not a given species has spread to that region and is available for colonisation even if ecological conditions are suitable, and also in its effect on the physical and chemical factors such as climate (temperature and rainfall etc.) and the geology of the land, which is reflected in the chemical composition of the water.

Rainfall may affect the degree of permanence of the streams and is important in determining the velocity of the current, which not only has a direct effect on the flora and fauna, but, as is well known, determines the type of stream bed by its action on the geological formations and by transporting or depositing the products of this weathering or loosening. In this, a time factor is concerned, for the precise nature of a reach of stream varies with its age and whether or not rejuvenescence has occurred.

Concerning the chemical composition of the water, there is still much to be learnt about the range of the balance of salts suitable for the various fresh water organisms and the effect on their distribution and density. For instance, calcium content of the water appears to be of importance, possibly not merely in its own right but as an index of the general trophic state of the water. PH range may also be of importance — either directly or indirectly — and the oxygen content of the water. Temperature range too, has

Table 4. Summary of physical and chemical data for the main sampling stations.

	Ceirw A	Ceirw B	Merddwr A	Bråån A	Skogsmöllebäcken
Longitude	4° W.			13° E.	
Latitude	53° N.			55° N.	
Approx. altitude in metres	169			89	93
Approx. width of stream in metres	7	7	4	7	3 to 4
Range in cm./sec. of average surface velocity of water over sampling area at times of sampling	30 to 110	45 to 175	30 to 90	24 to 90	30 to 70
Range of water temp. in °C. at times of sampling	1 to 16		1 to 16	0 to 23	0 to 24
pH	7.2 to 7.3		7.1	7.0 to 8.2	7.5 to 8.2
Calcium content of water as Ca in mg./l.	8.9			57.1 to 71.4	31.0
Range of dissolved O_2 in mg./l. at times of sampling	9.6 to 16.1			6.8 to 14.2	8.0 to 14.0

a direct influence on the nature of the plants and animals which a stream is capable of supporting, and on the rate of growth of these organisms.

The various physical and chemical factors interact in determining the nature of the plant growth, and this, by providing shelter and food, largely determines the nature and density of the fauna.

The interactions of these various environmental factors on the animal organisms are complex and sometimes one, sometimes another may become a limiting factor in determining distribution and density.

In the Welsh-Swedish survey, geographical location precluded the presence of certain forms in the Welsh streams and of others in the Swedish streams. For instance, *Perla carlukiana* KLAPÁLEK, *Chloroperla torrentium* (PICTET) and *C. tripunctata* (SCOPOLI), *Leuctra geniculata* STEPHENS and *L. inermis* KEMPNY, *Rhithrogena semicolorata* (CURTIS), *Glossosoma boltoni* CURTIS and *G. vernale* (PICTET) all occurred in the Welsh samples but are unknown in Sweden. Similarly *Isoperla diffiformis* (KLAPÁLEK), *Chloroperla burmeisteri* (PICTET) and *Elmis latreilli* BEDEL, which occurred in the Swedish samples, are not British species.

Table 4 summarises some of the physical and chemical factors for the various streams.

Southern Sweden comes under continental influence and has a more extreme climate than does North Wales, as is shown in Fig. 1 where air temperatures from meteorological stations in the two regions are compared during the sampling period. The difference is reflected in water temperatures, the Swedish Bråån and Skogsmöllebäcken having a wider temperature range

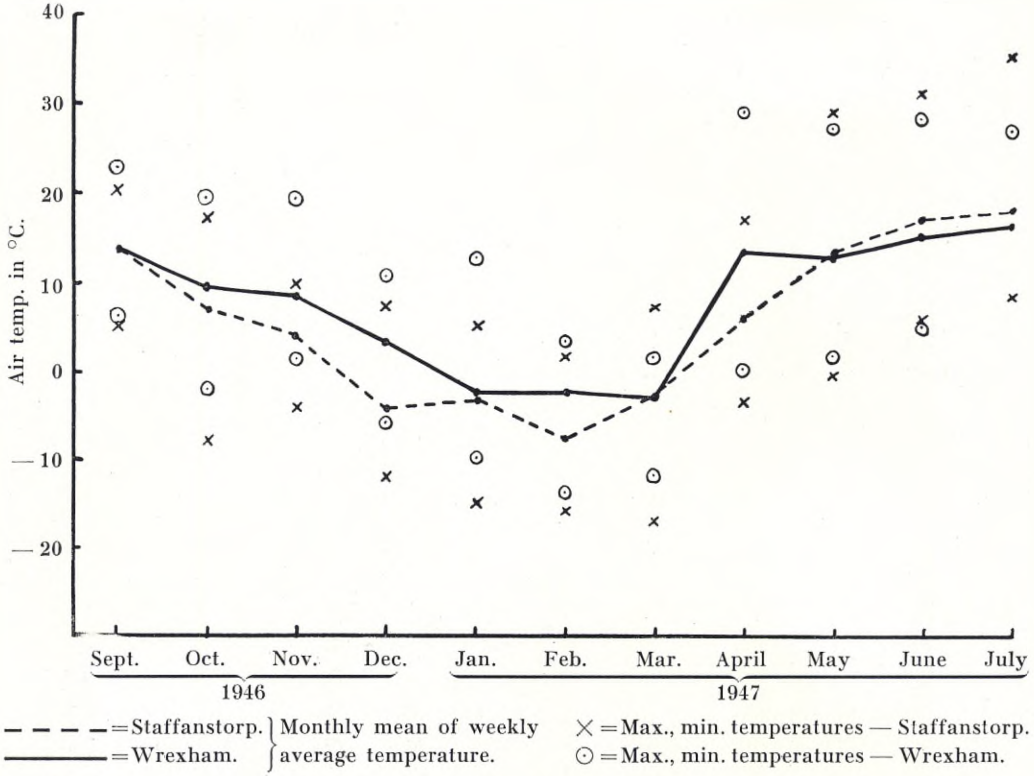

Fig. 1. Monthly mean, maximum and minimum air temperatures for Staffanstorp, Sweden and Wrexham, Denbighshire, September 1946 to July 1947.

(0 to 24° C) than the Welsh Ceirw and Merddwr (1 to 16° C recorded in 1946 to 47). The markedly warmer summer temperature in the Swedish streams may encourage some forms such as *Hydropsyche angustipennis* (Curtis) but it places certain others such as many of the Plecoptera at a disadvantage. Brink (1949) has shown that many of these grow only in autumn, winter and spring at temperatures ranging between 5 and 12° C. He lists only *Leuctra fusca* L. and *L. digitata* Kempny of the Swedish species as growing at summer temperatures. *Perla cephalotes* Curtis, known only from cooler streams, was absent from the samples and other perlids were infrequent.

Rainfall and rate of stream flow are probably important factors in this comparison. A lower rainfall in the Swedish area during the sampling period (fig. 2) and the existence of more wooded land in the upper reaches of the Swedish streams compared with the Welsh ones reduced the tendency to spates, resulted in lower normal water velocities (Table 4) and permitted the occurrence of more sheltered microhabitats. This was especially marked in the Skogsmöllebäcken where accumulation of »leaf packets» provided

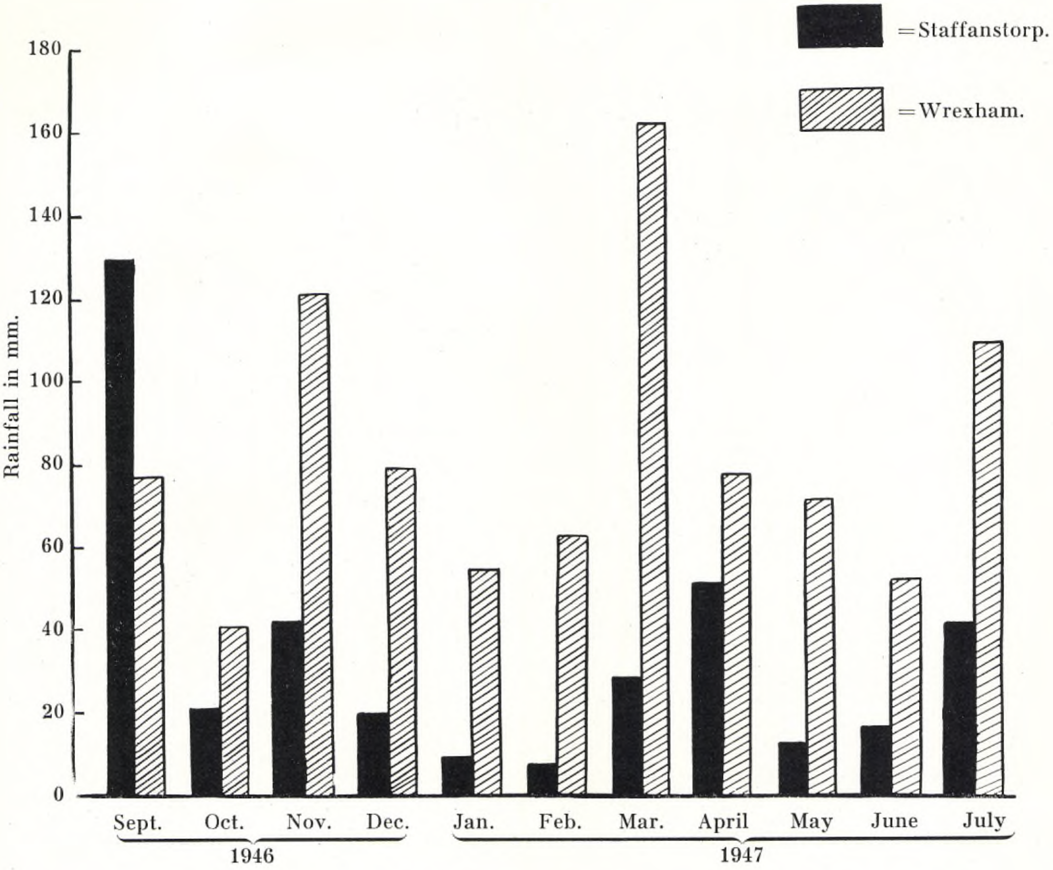

Fig. 2. Monthly rainfall for Staffanstorp, Sweden and Wrexham, Denbighshire.

suitable microhabitats for dense populations of *Gammarus pulex* L. and species of *Nemoura*. HYNES (1941) records certain *Nemoura* nymphs as occurring mainly in leaf packets in small stony streams or trickles.

The fairly moderate to gentle current and the absence of scouring spates, in both the Skogsmöllebäcken and the Bråån, may facilitate a dense population, including organisms which do not occur in fast currents. Thus larvae of the caddis *Phychomyia pusilla* (FABRICIUS) dwelt in the Skogsmöllebäcken and Bråån but were absent from the sampling stations in the Merddwr and Ceirw at Dinmael, although imagines were captured in the neighbouring area. This agrees with PERCIVAL and WHITEHEAD's (1929) observations in the Wharfe, where these larvae only occurred in slow currents.

Greater densities of *Polycentropus* in the Swedish than in the Welsh areas sampled may also be partly attributable to slacker water; the nets are delicate and larvae of *Polycentropus flavomaculatus* (PICTET) dwell mainly in fairly quiet microhabitats. They are carnivorous, eating small insect nymphs and larvae, so increased food supply may be another factor involved.

The water was well oxygenated at the main sampling stations and the oxygen concentration need not be further considered in this comparison. Ceirw and Merddwr water was soft (Ca=8.9 mg./l.) Skogsmöllebäcken harder (31 mg./l. Ca) and Bråån water hard (Ca=57 to 71.4 mg./l); pH ranges were 7.1 to 7.3 in the Welsh streams, 7.0 to 8.2 in the Bråån and 7.5 to 8.2 in Skogsmöllebäcken, the more alkaline conditions occurring during sunny summer weather when photosynthesis by the then abundant algae would be active.

The importance of calcium is reflected qualitatively and quantitatively in the mollusc population in this survey, although not as markedly as it might have been in heavily vegetated reaches of the Bråån. It is possible that the calcium content of the water, or perhaps the balance of salts has some direct chemo-physiological effect on other animals, but it seems more likely that in the majority of cases hard water influences the fauna indirectly by affecting the plant food supply. BUTCHER (1938) showed that the benthic algae were more abundant in a calcareous stream than in an acid one and (1949) that the density increases with progressive eutrophication of the water, i.e. with increase in its dissolved inorganic salts. The prevalence of *Cladophora* at the Swedish stations may be in agreement with this; the alga was so common that its collection was often unavoidable.

Observations on *Hydropsyche* indicate that the food factor and temperature are primarily important in accounting for the particularly dense population of these omnivorous larvae in the Bråån; very dense populations of the larvae of this caddis seem to be correlated with a good food supply — usually with either calcareous waters or with lake outflows (BADCOCK, unpublished).

Influence of the chemical composition of the water on the plant food supply may well be a factor with a widespread effect on population density, affecting the population not only of phytophagous organisms but also the carnivores which feed on this increased population of phytophages.

FROST (1942) in her survey of the moss fauna of acid and alkaline reaches of the Irish Liffey did not find much difference in total numbers of organisms at the two stations although there was a marked difference in composition. Her trends in distribution are paralleled in this survey to the extent that the *Plecoptera* and *Coleoptera* were of less importance in the most calcareous stream, the Bråån, than in the soft Welsh streams, while the *Ephemeroptera* and *Trichoptera* attained their greatest density at the Swedish stations. However in her survey, the habitat, sampling method and some of the species differed from mine. For instance, her stone flies were mainly moss dwelling species. Different factors may be involved in distribution in the two surveys; also it was small forms such as Copepods and *Cladocera* which increased the numbers at her acid station. These were not sampled in my survey — they may have been absent from the site or escaped capture.

In certain instances the plant life, including *Cladophora,* may increase population density by providing shelter, in addition to food. It may create not merely locally high concentrations of organisms within the shelter of the vegetation but also provide a source from which certain forms may extend to the stones, thereby increasing that fauna. This factor may influence especially the much greater density of *Ephemerella* in the Swedish than in the Welsh samples. PERCIVAL and WHITEHEAD (1929) found a richer *Ephemerella* population amongst *Cladophora* than amongst bare loose stones in the Wharfe. It is unlikely that *Cladophora* is correlated with the higher density of *Baëtis* in the Swedish streams, for *Baëtis* nymphs are generally less numerous amongst it (PERCIVAL & WHITEHEAD 1929).

Although salmon do not breed in the Kävlinge river system, they and sea trout have been planted out in large numbers in the hope of establishing them. In the Skogsmöllebäcken, the introduced salmon and sea trout augment a native fish population of brown trout and minnows; the Bråån, near the sampling station, has a natural population of eels, burbot, pike and minnows, while brown trout, sea trout and salmon fry have been planted out there. So it is unlikely that the denser invertebrate population in these Swedish streams is connected with relative paucity of fish predators.

Differences between the population have been discussed, but one should not overlook certain striking similarities. Although there may be differences in their population density, many of the same genera and even of the same species dwell in all the four streams considered. Animals common to the four streams include: —

Ancylastrum fluviatile (MÜLLER)
Gammarus pulex L.
Leuctra spp [*L. fusca* L. (=*L. fusciventris* STEPHENS) and *L. hippopus* KEMPNY]
Baëtis spp.
Ephemerella
Ecdyonurus
Caenis
Rhyacophila (differing species in the Welsh and Swedish samples)
Polycentropus flavomaculatus (PICTET)
Hydropsyche spp. (Some specific variation in the different streams.)
Hydroptila
Sericostoma personatum (SPENCE)
Goëra pilosa (FABRICIUS)
Silo pallipes (FABRICIUS)

Elmis
Hydraena gracilis GERMAR
Dicranota
Simulium

Chironomid (=Tendipedid) larvae, very abundant at all stations, were not determined, hence it is not possible to comment further on their detailed distribution.

Owing to the non-determination of chironomid larvae, community structure at the various stations cannot be fully depicted. According to LEATHERS (1921), while many chironomid larvae are phytophagous, those of the subfamily *Tanypodinae* are predacious, feeding especially on 'blood worms' and on small crustaceans, although they may also eat the more rapidly moving diatoms. The predominantly carnivorous tanypodinids appeared to be less numerous at the sampling stations than were the herbivorous *Orthocladiinae, Diamesinae* and *Chironominae*. Thus in general the abundant chironomid fauna can be considered as constituting one of the herbivorous keystones in the food-cycle, although within the group the component members constitute a small food chain. The other forms — i.e. *Leuctra, Nemoura, Baëtis, Ephemerella* and *Ecdyonurus* nymphs, *Hydropsyche* larvae, *Ancylastrum fluviatile* and *Gammarus pulex* — which come into the »more abundant» category at some or all of the stations are all herbivorous, with the exception of *Hydropsyche* larvae which are omnivorous but whose diet often includes a high proportion of algae. Food chains are discussed in further detail in an earlier paper (BADCOCK 1949) and it suffices here to indicate that the general concept of a pyramid of numbers with the predominantly phytophagous exceeding the omnivorous and predominantly carnivorous forms, holds true at all stations, although at the Swedish stations the carnivorous population can be greater than at the Welsh by virtue of the greater population of phytophages.

Summary

The problem of classifying streams for comparative purposes is considered. Owing to the great environmental complexity, existing classifications seem somewhat inadequate and often too arbitrary, but further work is needed on the influence of various factors on stream communities before a satisfactory classification can be suggested. Quantitative data on the fauna of different streams have to be treated with caution.

Nevertheless where methods and seasons are comparable, certain conclusions can be drawn from a study of the numbers of organisms in quantitative samples, a point illustrated by reference to samples from tributaries

of the Welsh Dee and of the Kävlinge river system in southern Sweden. These samples of fauna from stony stream bed indicated a denser population at the Swedish stations than at the Welsh and a decrease in the fauna in the winter samples from stones at all stations. Quantitative sampling also helped in assessing predominant organisms and depicting the stream community.

Various factors thought to be involved in differential qualitative and quantitative distribution are discussed with reference to these Swedish and Welsh stream. Important factors in this survey are considered to be: —

1. Geographical location.
2. Temperature range of the water.
3. Rainfall and topography, including extent to which the upper reaches of the streams are wooded, which affect current velocity, occurrence of spates, and types of microhabitats.
4. Chemical composition of the water.
5. Shelter provided by vegetation, e.g. *Cladophora* may increase the population density of certain organisms amongst stones by providing local concentrations from which they could radiate to the bare stones.

As the streams were well stocked with fish at all stations it is unlikely that the denser invertebrate population in these Swedish streams is connected with relative paucity of fish predators.

Despite certain differences, there are strong resemblances at the sampling stations — many genera and even species of animals are the same, and the community structure is essentially similar, the predominantly phytophagous forms being the most abundant and carnivores less numerous.

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Aquarium Observations on the Spawning Behaviour of the Burbot, *Lota vulgaris* L.

By Eric Fabricius

In Swedish lakes the spawning season for the burbot lasts from the end of January to the beginning of March. At this time the lakes are covered with ice, which prevents field observations on the behaviour of the fish. Consequently, nothing has been known about the spawning behaviour of the burbot, though this species during the spawning season is in many lakes the subject of intensive fishing, which is carried out with special type of fyke net placed on the spawning grounds.

In February 1954 an experiment with burbot was made in the same big tank, that had been used for studying the spawning behaviour of the char in the autumn of 1953. Zones with different bottom material, ranging from fine sand to fairly big stones, were arranged exactly in the same way as in the char experiment. For a detailed description of the tank and the arrangement of bottom material, the reader is referred to the account of this experiment (Fabricius and Gustafson 1954).

The experiment began on February 1st and was finished on February 15th. Four male and four female burbot, caught on some spawning grounds in Lake Mälaren, were released in the tank. The fish had been taken at a depth of 18 m, and consequently their air bladders had been expanded when the fyke nets were lifted up from the lake bottom. When introduced into the tank, they at first swam about at the water surface, and were not able to swim down to the bottom. After a period of time, which in different specimens varied from 2 to 24 hours, they had apparently regulated the pressure in their air bladders and began swimming about in a normal way. As it was observed that the burbot tried to find shelter between some big stones, a number of caves were made by placing slatestones over some crevices in the stony area. After this arrangement had been made, the burbot spent most of their time resting in the caves during the day. No fighting over the possession of caves was seen, and several specimens could rest in the same cave.

The first complete spawning was observed on February 5th, from 9 a.m. to noon. In an area with a fine sand bottom a male and a female were seen moving close to the ground. The female adopted a peculiar posture, in which she bent her head and tail upwards and tilted her body so that the head pointed down, while the tail was lifted. In this way she swam about at the bottom so that the barbel on her chin and the prolonged second fin rays of her pelvics dragged along the ground. It may be mentioned that this second ray of the pelvic fins was considerably longer in the females than in the males. The male swam in from behind under the belly of the female and placed his head under hers, so that her chin rested on his crown and her pelvics embraced his head at the region of the gills. In this posture the couple slowly swam about at the bottom, performing undulating lateral body movements. The intensity of these movements increased more and more, until a mating act followed. In mating the male suddenly rotated his body half a turn, so that his belly touched the vent of the female, and a large cloud of milt and eggs was ejected, while the couple swiftly swam forwards over the bottom.

After the spawning act the male and the female separated for a moment, and the female performed some movements which probably have the function of stirring up the eggs and the milt. She repeatedly flung her caudal fin laterally towards her head, so that she was propelled backwards along the bottom in a jerky manner, often turning herself on her side. As a result of this action, the water was powerfully stirred and the very light eggs were flung about and scattered over the wohle area of the tank.

After the stirring action the female resumed her tilted posture, the male again swam in under her lifted tail and a new mating act followed. The intervals between the successive mating acts varied from about 5 to 20 minutes. In addition to the complete acts, some incomplete acts occurred, in which the fish performed the same movements as in normal spawning, but without ejecting any sexual products. Some of these incomplete acts were followed by the stirring movements of the female.

Several times other burbot approached the spawning couple, but the spawners never attacked or threatened the intruders. On some occasions the female was followed by two males, but as one of them swam in under her belly, the other one abandoned her after a while, taking shelter in the caves. The total lack of aggressiveness in the adult spawning burbot was remarkable, considering the fact that I have seen young burbot, in their first summer of life, fighting vigorously over the possession of caves and crevices between stones and rocks in an aquarium.

At noon the female, looking totally spent, was abandoned by the male, which returned to one of the caves. For about two hours the deserted female remained on the sand bottom, alone swimming about there in the tilted posture of readiness, and on one occasion she was seen performing the stirring activity. No more spawning was observed in this pair, but on February 6th at 6 p.m. a second spawning couple was seen, and a third couple spawned on February 12th in the morning. On February 15th all the fish were spent and the experiment was finished.

Though the females were seen swimming about in a searching manner in the whole of the tank, all the spawning which was observed took place on the sand bottom, and only at this place the females adopted the tilted posture of readiness. The sandy area, covering sections VI and VII of the bottom used in the experiments with char, measured 2 square meters, and a detailed description of it has been given elsewhere (FABRICIUS and GUSTAFSON 1954). It can be mentioned that most of the known spawning grounds for burbot in Swedish lakes consist either of sand or of hard and smooth clay bottoms.

At the lake bottom, where the burbot spawn under the ice, the water temperature is about 4° C, or sometimes lower. The actual temperature measured on the spawning grounds where the burbot were caught was 3.2°. In the tank the temperature was 7.0° at the beginning of the experiment, and then it was gradually cooled down to 2.8°, which temperature was reached on February 15th. The first of the three pairs, which spawned at the bottom in a normal way, spawned at 4.0°, the second at 3.8° and the third at 3.0°. But, as will be mentioned later on, one pair of burbot performed some mating acts at the water surface as early as February 2nd, when the temperature was 6.5°, and spawning thus seems to be possible in aquaria in water which is much warmer than at the natural spawning grounds. Similar observations have been made in other species of fish as well (FABRICIUS and GUSTAFSON 1954).

All observed spawning took place either in the morning or in the evening. During the day the burbot rested in the caves, as already mentioned, but at night they were very active, swimming about in the tank, and as many eggs were found in the mornings, it seems possible that some spawning occurred at midnight. In an aquarium experiment described by OWSIANNIKOW (1885) a pair of burbot spawned only at night, which apparently made it impossible for the experimenter to observe their behaviour. A 60 watt bulb in the ceiling of our observation chamber did not disturb the spawning burbot, but when a stronger bulb of 500 watts was switched on over the tank, the fish suddenly took shelter in the caves, making photographing impossible. They did not leave the caves until this intense light had been switched off.

The tilted posture of the female burbot is of some interest. When the female lifts her tail, she displays her swollen belly to the male, which swims behind her. Most probably this attitude is a signal movement or social releaser (TINBERGEN 1939, 1948), and it may be mentioned that signal movements in which the female, when ready to spawn, displays her swollen belly to the male, are known in at least two other species of fish, viz. *Gasterosteus aculeatus* (TER PELKWIJK and TINBERGEN 1937) and *Gobius microps* (NYMAN 1953). When lifting her tail the female burbot not only displays the contours of her enlarged belly, but also shows the only conspicuous colour contrasts which exist in the markings of this species. The burbot does not develop any nuptial colours. During the spawning season the fish retains its usual colours, in which the head, the back and the sides are dull brown sprinkled with darker brown or black spots, while the belly is light grey, or almost white. By tilting her body the female in her posture of readiness displays this light belly to the male, which reacts by swimming in under it. It might be of some interest to note that spawning burbot are caught in a sort of hanging fyke net, in which the opening is turned down towards the bottom, and that some fishermen are of the opinion that they get more burbot if they fix some pieces of white birch-bark to the opening of the trap.

The importance of comparative ethology has recently been emphasized by LORENZ (1950), who already in some of his earlier papers (1932, 1935, 1939) has pointed out that some elements of mating behaviour and courtship often behave in a very conservative way in the evolution of animal species. In the northern hemisphere the burbot is the only freshwater species of *Gadidae,* and apparently it has been isolated very early from the numerous marine species of this family. A comparison between the spawning behaviour of the burbot and that of the marine representatives of *Gadidae* would thus be of great interest, and of the latter the cod (*Gadus callarias* L.) is, as far as I know, the only species in which the spawning behaviour has been watched.

This aquarium experiment was made by ROLLEFSEN (1932), who gives the following brief description: »I also had the opportunity to see the copulation of the cod. At a first step the male was swimming with his head resting on the crown of the female, gradually he sank sideways, and finally male and female were swimming belly against belly, while the eggs and the milt were being whirled together by the vigorous movements of their tail fins.» (ROLLEFSEN, op.cit., p. 34). In addition to this account, Rollefsen in a personal communication has kindly told me some other details. No posture of readiness could be observed in the female. The male just approached her and pushed his snout against her flank. Then he placed his chin on her crown, and in this posture the couple swam about for some minutes. After this he gradually sank down along the side of the female and a mating act followed, in which the male swam under the female, turning his back downwards and pressing his belly up against hers. In this posture the pair rapidly swam forwards, expelling their sexual products, and the eggs and the milt were powerfully stirred by the water movements made by the tail fins of the swimming fishes.

The similarities between the cod's and the burbot's spawning activities are striking. In both species one of the fish rests its chin on the crown of its partner, though the upper position is taken by the male in the cod but normally by the female in the burbot, and in both cases the male in the actual mating act rotates his body so that he turns his back downwards and presses his belly against the female's vent. The most important differences are the lack of a conspicuous posture of readiness and of special stirring movements in the female cod.

It is a well-known fact that the very light eggs of many gadids contain drops of oil, which make them more or less floating. As described by ROLLEFSEN (op.cit.) and others, the cod of the Lofoten islands spawn in a pelagic manner in the free ocean water, in a transitional layer between the warm Atlantic water in the deep and the cold surface water, and the eggs float about in the water until they hatch. The burbot eggs are very easily carried about by water currents, but in still water they finally sink down to the bottom. In our aquarium most of the eggs had sunk down about 24 hours after the spawning, but in an experiment with artificially fertilized burbot eggs, described by WESENBERG-LUND (1908), a few eggs were still floating after four days. The incubation period is, however, much longer. At +4° C the eggs hatch after four to five weeks (EHRENBAUM 1909), and at +2° C after 41 days (VALLIN 1942), which means that they must sink to the bottom in any case before hatching. In the lakes the burbot eggs would, of course, come in contact with the ice, and perhaps get stuck to it, if they did not sink.

One could, perhaps, suppose that the fact that the eggs sink has made it necessary for the burbot to spawn on clean and smooth bottoms, where the eggs do not get covered with mud and die from lack of oxygen, and on such bottoms the females perform a signal movement to which the males react by approaching and mating. The specialized stirring movements probably have developed to scatter the eggs in the still water under the ice, where almost no currents occur which could carry them about. If this is true, one could say that the burbot in its spawning has maintained the basic behavior patterns of the marine gadids, but in addition, as an adaptation to the freshwater environment, it has some specialized activities.

Finally some observations should be mentioned to show that the burbot, under some abnormal conditions, can be forced to display almost exactly the same spawning behaviour as the cod. As previously mentioned, the burbot shortly after having been introduced into the tank were not able to dive down in the water, apparently because their air bladders were inflated. On February 2nd a female in this condition was floating at the surface of the water. A male, which already swam normally, approached her and swam along her flanks, pushing his head against her body. Repeatedly his head glided up on the crown of the female, and on two of these occasions he rapidly rotated his body, pushing his belly under the vent of the female and expelling a large cloud of milt. Simultaneously the female squirted out a lot of eggs as well, but no stirring movements were seen after these abnormal spawning acts.

Summary

The spawning of the burbot was observed in an aquarium. The female slowly swam about on a sand bottom in a tilted posture, with lifted tail and her head pointing downwards, dragging the chin barbel and the prolonged second rays of the pelvics along the ground. The male approached her from behind, swam in under her belly and placed his head under hers, so that her chin rested on his crown. In this posture the couple swam about at the bottom for some minutes. Then the male suddenly rotated his body half a turn, pushing his belly against the vent of the female. In this mating act a cloud of eggs and sperm was released. After mating the male and the female separated for a moment, and the female performed a series of powerful tail beats which stirred up the sexual products and scattered the eggs. The eggs were carried about by the water movements caused by this activity, but they finally sank down to the bottom. After the stirring activity the female resumed her tilted posture, the male again swam in under her belly, and a new mating act followed. In this way the spawning went on with successive mating acts until the female was spent.

Three spawning pairs were watched, and all spawning took place on sand bottoms. The burbot did not defend any territories, and no aggressiveness or threatening were observed. The fish were photophobic, taking shelter in caves when subjected to intense light.

The function of some of the spawning activities is discussed. Some similarities between the spawning behaviour of the burbot and the cod are described.

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Further Aquarium Observations on the Spawning Behaviour of the Char, *Salmo alpinus* L.

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1. Introduction

Our observations on the spawning behaviour of the char made in 1951 and 1952 (FABRICIUS 1953 a and c) were in some respects incomplete. The tank used was so small that the territorial behaviour could not be studied properly. The covering of the eggs was not observed, and all details of the spawning act could not be recorded, because the spawning took place under poor light conditions.

In September and October 1953 the studies were followed up by experiments made in a new larger tank. This aquarium measures 7 meters in length, 1 meter in width and 80 cm in depth. One of the longsides, facing the wall of the aquarium building, is made of an opaque grey material called »eternit». Seven plate glass windows are incorporated in the other long side, facing the observation chamber. Each window is 97 cm long and 50 cm high. The short ends of the tank are also provided with windows of the same dimensions.

During the experiments, the depth of water was kept at 35 to 45 cm. Before the water reached the aquarium, it passed through a container in which was immersed a refrigerating coil, controlled by a thermostat. Thus, it was possible to maintain the temperature in the tank at any level between 3.5° C and that of the room. The tank is fitted with an overflow pipe leading into a basin, from which the water is pumped back to the cooling container. Thus, there was a constant flow of water through the aquarium, but the velocity of this flow was so low that no real current or stream could be observed in the tank. Floating objects were not carried along the tank by any directed water movements, and the water in it could be regarded as practically still.

The bottom of the tank was covered with a layer of sand, gravel and stones, the depth of which was approximately 5 cm at the front panes and 15 cm at the rear wall.

From the point of view of fishery biology, it was of particular interest to discover what bottom material the females preferred for nest-digging. In the observation tank we arranged seven zones or sections with different bottom material, ranging from fine sand to fairly big stones. Beginning from the left end of the tank, the bottom material in these zones was as follows:

I. Fine sand (grain diameter below 0.6 mm), planted with sparse groups of *Isoetes lacustris.* Fishermen believe that the char in some Swedish lakes spawn on bottoms covered by *Isoetes*-plants. This section was the only one which had some vegetation, all the other sections being barren.

II. Fine gravel (grain diameter 1—1.5 cm).

III. Coarse gravel (grain diameter 2—6 cm). This bottom was characterized in our preliminary papers as consisting of »stones of walnut-size» (FABRICIUS and GUSTAFSON 1953, 1954).

IV. A rocky bottom, built up of stones, the diameters of which were 10—25 cm. There were two layers of these stones, so that the fish, when swimming over this bottom, could not see any other material in the spaces between the rocks.

V. A »mosaic» bottom, on which small patches of sand and gravel were visible between a number of rocks, the same size as those in section 5. None of the patches of finer material had a diameter of more than 10 cm, and thus they were not big enough for making nest pits.

VI. Coarse sand (grain diameter up to 5 mm).

VII. Fine sand (grain diameter below 0.6 mm). The size of each of these zones was one meter square, and each of them faced one of the front panes. The fish had free access to all the zones.

Two experiments were made with a total number of 40 char, caught in the mouth of the River Blåsjöälven at Lake Jormvattnet in the province of Jämtland. In each experiment 20 char were used, 10 males and 10 females, and all these specimens were judged to be ripe or almost ripe when they arrived. In the first experiment the fish were released in the tank on September 25th and removed on October 2nd. The second experiment began on October 3rd and was finished on October 10th. A third experiment, made with a small number of char from Lake Vättern, is described on page 91.

During the experiments a ciné film of the whole spawning behaviour of the char was made by one of us (K.-J. G.).

A brief preliminary account of the 1953 experiments has already been given by FABRICIUS and GUSTAFSON (1953, 1954). A more detailed description of our observations follows.

2. Territorial Behaviour

After having been introduced into the big tank, the char at first swam about forming a dense school.

In both experiments the males were the first to show aggressive behaviour. This was observed after 40 minutes in the first and after 55 minutes in the second experiment. At first some occasional attacks were observed, but soon fighting and threatening males were seen at many places in the tank.

For a description of the threat postures the reader is referred to our previous papers (FABRICIUS 1953 a and c, FABRICIUS and GUSTAFSON 1953, 1954). In our earlier experiments we got the impression that the adult char only dilates the lower parts of the mouth bottom very slightly in the threat display. This was probably due to the fact that the threat display was of a rather low intensity in the small tank where no real territorial behaviour could occur, for in the big new tank the downward pressing of the mouth bottom was very marked in the threatening char. This was the case both in the frontal and the lateral type of threat display. In adult char, during the spawning season in particular, the lower parts of the branchiostegal membrane and the area between the two dental bones are sprinkled with dense groups of black pigment cells, making these parts almost black in colour. The lower jaws are usually white or lemon yellow, and in the threat display this light colour of the jaws contrasts very conspicuously with the black of the lowered mouth bottom, as can be seen in the attacking male in fig. 10 in one of our previous papers (FABRICIUS 1953). This colouration is quite the reverse of the colour patterns in the young char and the brown trout, where the mouth bottom is white and the rest of the head is dark (FABRICIUS 1953 a, b, c).

A mutual lateral display, in which two males swam side by side with the head and tail slightly bent upward, the mouth bottom lowered and all the fins maximally erected was seen more frequently than in our earlier experiments. Two males in this act could sometimes travel the whole length of the tank, passing through the territories of several other males. A similar behaviour in the males of *Oncorhynchus nerka* has been called »escorting» by SCHULTZ (1937).

It was sometimes seen that a char made an attack without any preceding threat display. This was particularly common in very sudden attacks and when a fleeing opponent was chased. The most intense threat display occurred in prolonged fights.

A fleeing char could often make a sudden flap with its tail, throwing a jet of water against the pursuer. This movement is probably the same which the atlantic salmon uses when, according to JONES and KING (1950, 1952), it drives an opponent away by swimming some feet upstream dropping backwards from this point, tail first, towards the adversary driving it off by flapping the tail laterally ahead of its snout. In both cases the fish which flapped its tail was ahead of its opponent and the distance between the two fish decreased, though this happened in the cases described by JONES and KING (op.cit.) because the water current carried the first fish backwards, whereas in the case of the char the distance between the two fish diminished because one of them was chasing the other. Probably this tail flap is released in a fish when an opponent is behind it coming in close proximity to its tail.

Displacement feeding, in which a fish took a small stone or some sand in its mouth and then spat it out again, was frequently seen in fighting males. In the 1951 and 1952 experiments we had observed this behaviour in females only.

After 45 minutes in the first experiment and one hour in the second, it was observed that some males defended well-defined territories, and in the first experiment the whole area of the tank was soon divided into such territories. Unlike our 1951 and 1952 experiments, there were no periods of inactivity in the territory-guarding males, at least not during the first days of the experiments. They cruised restlessly about in their territories, violently attacking all trespassers. By means of these attacks they were very well able to keep their territories free from other char, except on some occasions when territories were temporarily invaded by whole swarms of trespassers. During the first three days of the first experiment, when the territories occupied the whole area of the tank, other fish were often tolerated within the territories while resting on the bottom, but they were attacked as soon as they moved. For most of the time a part of the tank was left free from territories, and then all the fish, which had no territories, were driven together in this neutral zone.

There are some differences between the territorial behaviour of the char and that of, for example, cichlid fishes. Territory guarding cichlids keep strictly to the boundaries of their territories, and they immediately stop as soon as they pass them (BAERENDS and BAERENDS 1950). The char keep strictly to their territories as long as they just are cruising about in them, but when chasing an opponent, fighting or threatening, a char may pass through the territories of several other specimens.

As a rule every territory-guarding male remained in his territory for several days, though there were some exceptions. It sometimes happened that a male, whose territory was situated between those of two very aggressive specimens, abandoned it and either completely gave up his territorial behaviour or occupied a new territory in another part of the tank. Later on, when the females had begun digging nests, it also happened that a male abandoned his territory and joined a female in her nest somewhere else in the aquarium. If a male was removed for some minutes or for a few hours, for example for photographing, he returned as a rule to his territory when he was again released in the aquarium, even if he was introduced at the opposite end of the tank. Sometimes the returning male had to fight another male which had occupied his territory during his absence, and in most cases the former territory owner succeeded in driving the newcomer away.

In the first experiment 2 males showed territorial behaviour for 8 days in succession, 2 other males defended territories for 4 days, 2 for 3 and 3 for 2 days, while one of the males did not show any territorial behaviour at all.

In the second experiment 2 males guarded territories for 5 days, 2 for 3 and one for one day, while the remaining 5 males in this experiment did not show any territorial behaviour.

The above numbers of territory-guarding males includes some specimens, which defended territories only on occasions when some of the other males were temporarily removed from the tank.

During the first three days of the first experiment there were 4 territories in the aquarium and, as mentioned, they covered the whole area of the tank. Some of the other males made occasional attempts at establishing territories, but without success. One of these males succeeded in defending a fifth territory for a few hours, but his territory diminished more and more in size, and at last he abandoned it and ran the gauntlet in the tank, violently attacked and chased by the other four territory owners.

During the first two days of the first experiment we twice removed all the four territory owners and transferred them to a smaller thank, which was 215 cm long and 57 cm broad. In both cases one of the males, after a series of fights, dominated the other three and guarded the whole little aquarium as his territory. This situation was established after 1 $^1/_2$ hours in the first and after 4 hours in the second of these experiments.

The first time the territory owners were removed, 4 new males almost immediately began to defend territories in the big tank. When the former territory owners were brought back to the big tank, two of them reoccupied their old territories, but two of the new territory owners succeeded in keeping their territories, and one of them was the fish which after some hours dominated the others when all the territory owners were transferred to the small tank for the second time. This time only 3 new males began to guard territories in the big tank after the removal of the former territory owners, and two of them were the two fish which had not succeeded in reoccupying their territories after having been temporarily removed from the tank in the previous experiment. When for the last time the four fish from the small aquarium were brought back to the big tank, only one of them reoccupied his territory, and this was not the fish which had been the dominating one in the small tank, but it was one of the specimens which had taken a territory in the big tank the first time the old territory owners were removed.

These experiments showed that a maximum number of four territories could exist in the big tank, while there was only room for one territory in the small aquarium, the bottom area of which was about 1.2 square meters. The actual size of the territories observed in the big tank varied from about one to about three square meters, and their average size could be calculated as about 1.7 square meters. It can be mentioned that the mean body length of the 13 territorial males was 30.2 cm (27.5 to 37.0). No regular relation between the body size of a fish and the size of its territory could be observed.

The experiments demonstrated the fact that real territories can only be established in a tank whose bottom area is at least twice the minimum size of a normal territory. If the size of the aquarium is smaller than that, a sort of peckorder develops, in which one fish dominates the others. Similar observations have been made in other species of fish, for example sticklebacks (WUNDER 1930, TER PELKWIJK and TINBERGEN 1937, MORRIS 1952), sunfishes (BREDER 1936, GREENBERG 1946, 1947) characinids (MEYER-HOLZAPFEL 1941) and cichlids (BAERENDS 1950).

On the fourth day of the first experiment the number of territories had been reduced to three. On the fifth and sixth days two territories existed, whereas on the seventh day only one territory was still defended.

In the second experiment 3 territories existed during the first and second days, and two during the remaining three days, but some of the males had long periods of inactivity during which other males could be active. The number of males, which on a given day showed territorial behaviour could thus be greater than the number of territories existing simultaneously.

It could not be observed if the individual territories increased in size when their number decreased, but this can have been because all the males had then formed pairs with spawning females and were more interested in them than in distant males. It was, however, striking that the largest territories were found in the most open areas I, II, VI and VII, where no ground obstacles provided any visual isolation (cf. FABRICIUS 1951).

Some females which had not formed pairs with any males, nor begun their nest-digging, were occasionally seen defending territories, cruising in them like males. This was particularly common in the second experiment, when the number of male territories was small. When the nestdigging had begun, the females always defended the area round the site where they were digging.

3. Some Experiments on Visual Stimuli Releasing Aggressive Behaviour

In our earlier experiments some observations had been made, which caused us to expect that the red colour in the spawning markings of the char would be one of the releasing stimuli for attacking (FABRICIUS 1953 a, c).

In our 1953 experiments we observed that territory-guarding males, as well as females defending their nests, attacked moving models of almost any size, shape and colour. A series of experiments was made with three cardboard discs of an oval shape, which were 16 cm long and 5 cm broad. One of the models was red, another was black and the third was white. When the models were moved outside the pane, in front of a territory-guarding char, they were often attacked most violently by the fish, which rushed against the front pane with open mouth and fins erect. In the series of experiments the models were shown in succession, with an interval of one minute between each exposure, until each model had been shown 100 times. The same territory-guarding male was used in the whole of this series of experiments. Tab. 1. shows the result of these experiments.

In Tab. 1. »Approached» means that the fish swam towards the model but turned round before it reached the front pane, whereas »Courted» means that the male turned its flank against the pane in front of the model and performed the trembling body movement which is characteristic of courting. The models were moved so close to the pane that they almost touched it.

The figures indicate that the red model was evidently the most effective in releasing attacks, and thus the red colour actually seems to be one, though certainly not the only one, of the visual sign stimuli belonging to the releasing mechanism of the attacking behaviour in the char. Probably the movements

Tab. 1. The behaviour of a territory-guarding male char towards three coloured models, each of which was shown 100 times. The figures indicate how many times each type of behaviour was recorded.

Colour of the model	Treatment			
	Ignored	Approached	Courted	Attacked
Red	24	11	4	61
Black.........	37	20	4	39
White	42	27	3	28

of the models also stimulated the aggressive behaviour, for models were rarely attacked if they were kept motionless. As mentioned moving objects of almost any shape, size and colour are attacked. For example, we have seen territory-guarding males attacking air bubbles rising from the bottom material. Some observations indicate that the releasing mechanism must also react to some features, which living fish and our models did not have in common. Thus it was observed that the territory-guarding male also attacked other males during periods when it did not attack any of the models. Probably the attacks are released under natural conditions by a heterogeneous summation of several stimuli (cf. TINBERGEN 1948), one of which is the red colour of the opponent's belly.

The male used in these experiments was one of the specimens from Lake Vättern, whose spawning is described on p. 91. Experiments with some of the males from the River Blåsjöälven indicated that they too attacked the red model more frequently than the black or white ones.

4. Nest-Digging

The nest pits were only dug by the females. Before a female began digging, she always showed a peculiar »searching», behaviour, which was also seen in our 1952 experiments (fig. 1). With her head and tail slightly bent downwards she swims slowly about along the bottom, and her eye movements clearly show that she examines the ground. The first searching female was observed after 2 $^1/_2$ hours in the first experiment and after 1 hour in the second.

When a female had begun the searching, she maintained her typical searching posture as a rule during the whole period of nest-digging and spawning. After some time the searching females always began to show preference for a certain bottom area, remaining there and swimming about in the searching manner only at this particular place. When several females were searching close to each other, vigorous fights between them were seen, and approaching males were also attacked.

Sooner or later the female begins digging somewhere in the area, which she has chosen during her searching. In the first experiment the first digging was observed in the afternoon of the second day, while in the second experiment a female began digging on the first day, about 4 hours after she had been introduced into the tank.

The female char has two different types of digging movements. In the first type of digging she remains on the spot and, without turning herself on her side, performs very rapid and powerful swimming movements, flinging a jet of water backwards, which sweeps sand and other loose material away. This movement could perhaps be called sweeping. Though 18 digging females

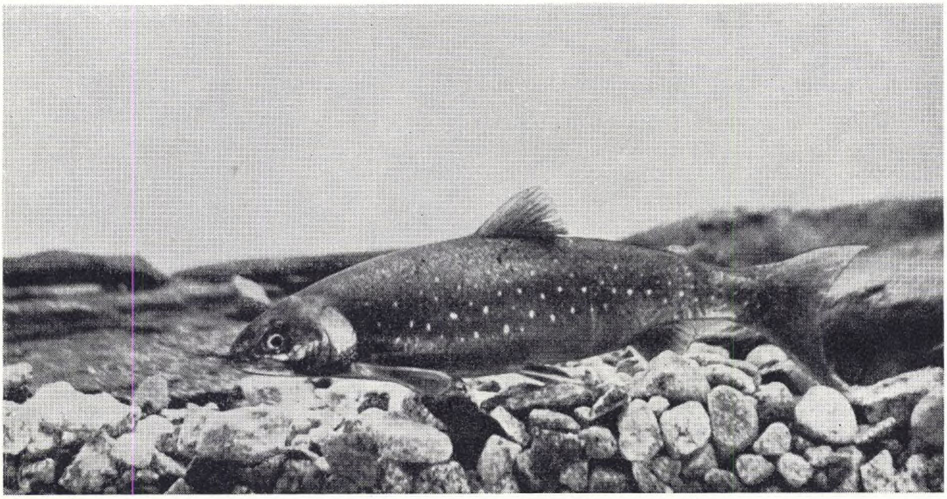

Fig. 1. Female char in the posture typical of the searching for a digging site. — Photo: K.-J. GUSTAFSON.

were watched, sweeping was observed in only 5 of them, and in these specimens it also occurred much less frequently than the other type of digging. However we succeeded in getting some cinematographic records of sweeping. This movement was performed both on stone, gravel and sand bottoms.

The other digging movement, which is the most frequently used and also the most effective, is of the common salmonid type. As has been briefly described in our previous papers, the female turns over on her side and performs a series of vigorous flapping movements with her tail.

A close study of some slow-motion shots from the 1953 ciné film enabled us to analyse this movement in greater detail. The fish at first swims slowly forwards in the searching posture. The tail swings rather slowly from side to side, so that the anal fin sweeps over the ground. The dragging anal fin is kept slightly erect, moving over the stones like a ratchet. It is pressed together every time it glides over the top of a stone, and is suddenly erected again after passing over the obstacle.

After having passed over a certain area a number of times in this way, the fish begins digging. Unlike the atlantic salmon, as described by JONES and KING (1950), the female char did not start, at least in the cases recorded in the ciné film, by rotating her caudal fin so that it rested flat on the ground. She began by bending the caudal part of her body laterally, so that her tail was pulled forward. Simultaneously she bent her head to the same side to which her tail was pulled. At the beginning of the movement her caudal fin had its normal vertical position, as shown in fig. 2, but because its lower portion dragged along the ground, it was gradually rotated while pulled for-

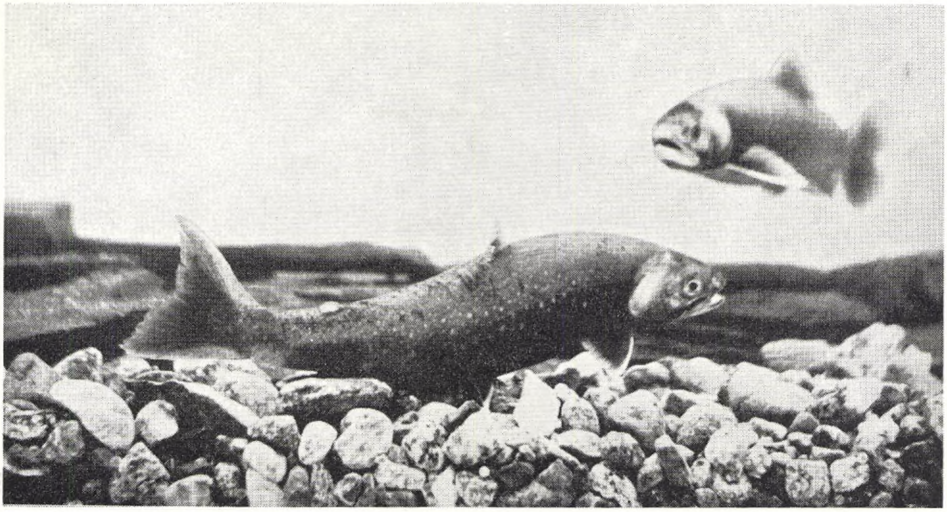

Fig. 2. Female char in the initial phase of digging. The body is bent in an S-shape, but the caudal fin is still not rotated. In this case the action contained some elements of »anchoring» (p. 79), which is shown by the fact that the anal fin is lowered very deep into a crevice, and the fore part of the body is slightly erected. — Photo: E. FABRICIUS.

ward. Another result of the dragging was that the tip of the fin »lagged behind», so that in the final phase of the movement it pointed slightly backward. At this stage the mid-dorsal line of the fish and the dorsal edge of the caudal fin formed an »S». Sometimes the rotation of the body began already during this first downstroke (JONES and KING 1949), but often it did not begin until the subsequent upstroke. In the upstroke the fish, from the position described above, performs a very rapid and powerful straightening of the body. During this movement the rotation of the body is completed and the fish is propelled forward. Maintaining her position with the flank turned towards the ground, the female makes a rapid series of new downstrokes and upstrokes. As a result of this action, the fish is propelled forward, while material is loosened from the ground and flung backward.

During the digging movement the pectoral, pelvic, anal and dorsal fins of the female are erected and her mouth is open, though not as wide as in mating and high intensity courting. JONES and KING (1950) have ovserved this opening of the mouth and erection of the fins in the digging in the female atlantic salmon as well.

In a few cases it was observed that in very ripe females, some eggs were liberated during the digging movements. This abnormal egg-dropping can, as was observed in our 1951 and 1952 experiments, also occur under other circumstances than digging. In our 1953 experiments it was very frequently seen in three apparently sick females, which did not spawn. Eggs just dropped

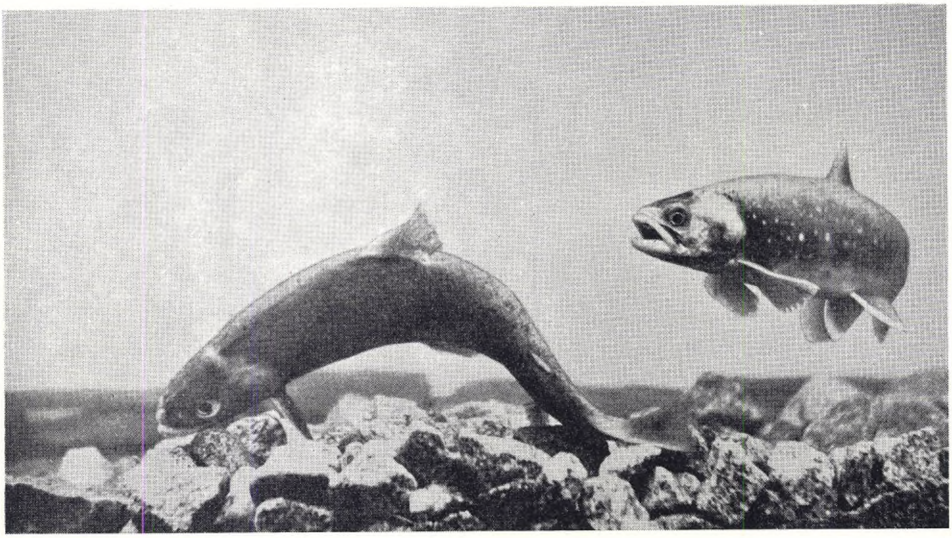

Fig. 3. Female char digging, attended by the male, which incessantly swims in circles round her. — Photo: K.-J. GUSTAFSON.

out when they swam about, and other fish swam behind them, swallowing the eggs as they appeared.

One of the effects of the digging movements is that loose material is sucked up from the ground. This was very clearly demonstrated when a female dug in section V, at a place where the bottom was covered with fairly big stones which were partially embedded in sand. The crevices between the stones were so narrow that the tail of the digging fish could not come in direct contact with the layer of sand. The female performed her digging movements on top of the stones, and the result was that the sand between them was sucked up and flung away. When this female had finished her digging, one could see a circular patch where the stones were cleaned and the crevices between them had been made very deep, and this patch was surrounded by a wall of sand, forming a ring and covering the stones of the periphery.

In the upstroke the material which is flung backward is mainly carried by the jet of water caused by the powerful movement of the caudal fin, as has been stated by JONES and KING (1949, 1950), but on some occasions it was also clearly seen that during the beginning of an upstroke the tail fin cut under a small stone and threw it up actively. This happened particularly often when a fish dug on coarse gravel.

After digging the female usually swims forward and, moving in the typical searching manner described on p. 65, she turns in a circle, returning to the place where the digging has been performed. There she often turns over again on one side and makes a new series of digging flaps, and so she continues often for several hours. Sixtysix minutes of timed observations of digging females gave a mean of 0.8 digging acts per minute, but in very intense digging some females could perform as much as one digging act each 40th second.

Often one gets the impression that the female starts her digging movement each turn at a particular stone, just when her dragging anal fin, moving like a ratchet, has passed over this object. Close observations of a female, which dug at the front pane, showed that this is not always the case. This specimen repeatedly dug on a row of stones, parallel to the front pane. The stones were numbered 1—11. A group of eggs was lying in the crevices between stones 1—4, and the digging observed was a »cutting made to cover up the eggs» (JONES and KING 1950). The female, which always swam in the same direction when passing over the row of stones, started her digging on stones 7—11 and after digging she turned round and, from stones 1—2, swam again in the searching manner back to the first mentioned stones. During 8 minutes she performed 13 successive digging acts. Each time it was noted at which stone she started digging, and the result was as follows: 11, 11, 8, 11, 11, 11, 6, 8, 7, 10, 11, 11, 10. Then the female and her attendant male performed three incomplete spawning acts at stone 9 and after that three complete spawning acts, one of them at stone 10 and two at 8.

The female char always digs before spawning, but the result of her digging depends on the bottom material. In sand and gravel rather deep circular pits are formed, on bottoms where stones are embedded in sand and gravel the stones are cleaned within a circular patch and the loose material between them is sucked up so that the crevices become very deep, and on rocky bottoms without any loose material one cannot see any result of the digging movements.

In species of salmonids, which spawn in running water, the material which is loosened by the digging flaps is partly carried away by the current. The experiments with the char show that the digging movements are also effective in still water. As a rule the females, which were about 30 cm long, were able to throw up stones measuring up to 4 cm in diameter, but on one occasion it was observed that a stone measuring 9,5 cm in diameter and weighing about 600 gr (in the air) was displaced about 20 cm by the digging movements of a female, which was 32,5 cm long and weighed 460 gr.

5. Selection of Nest Sites by the Females

Of the 20 females from the River Blåsjöälven, 17 dug nests and spawned in the big tank. Table 2 shows the number of females which dug their nests in each of the zones with different bottom material, that had been arranged in the tank. For a detailed description of these zones, the reader is referred to p. 59.

Tab. 2. Selection of nest sites by 17 female char. The figures indicate the number of females which began their nestdigging in each of the zones in a tank, where 7 zones with different bottom material had been arranged.

Bottom material	Number of first nests
Fine sand with *Isoetes* plants. (Zone I)	0
Fine sand without vegetation. (Zone VII)	0
Coarse sand. (Zone VI)	1
Fine gravel. (Zone II)	1
Coarse gravel (Zone III)	9
Cobblestones. (Zone IV)	4
Stones embedded in sand. (Zone V)	2

Only the first nest of each female was taken in to account, because it sometimes happened that a female, after having dug her first pit, crossed the border to another zone when digging the row of subsequent pits.

This experiment on choice indicates that coarse gravel, consisting of stones roughly of walnut-size, was the favourite material for nest-digging, and that rocky bottoms were preferred to sand bottoms.

On the other hand, we have made some observations showing that sand is preferred to flat and smooth stones. In the 1952 experiments we had built up an area of flat disc-shaped slatestones, which were arranged in a manner like roofing tiles, so that the edge of each stone was partly hidden under the edges of the other ones, leaving hardly any crevices visible. This group of stones was surrounded by areas of sand bottom, and the females dug only in the sand (FABRICIUS 1953 a, c).

In making our film, which was done in the small tank, the measurements of which have been given on p. 62, we at first attempted to make use of these 1952 discoveries. We screened off the middle part of the tank by glass plates, and in this area we covered the whole bottom with flat stones, arranged in the same way as in the 1952 experiments. Only at the front pane, in the focus of the camera, we left a small patch of sand and fine gravel, measuring about 45×30 cm.

A pair of spawning char were introduced into this tank. The female swam searching about over the whole bottom, but she only dug on the patch of sand. She made a deep pit, but it took 13 hours before any spawning acts were seen. Most of the spawning acts were incomplete, and in the few complete acts the number of eggs was abnormally small.

When the observations in the big tank had made it evident that the females preferred coarse gravel, the bottom in the filming tank was rearranged. The flat stones were left intact, but the patch at the front pane was covered with stones of walnut-size, as seen in the photographs. Nine females, which were then introduced into this tank, all dug on the gravel patch only and spawned there in quite a normal way. They swam searching about in the whole enclosure at first, but soon showed a clear preference for the gravel patch, swimming searchingly about there, turning every time they reached the border between it and the surrounding flat stones, and after that they began digging in the gravel.

These observations in the small filming tank confirm that coarse gravel, consisting of walnut-sized stones, was the most favoured bottom material for digging, and that sand was preferred to flat stones between which no crevices were visible. These facts can be used practically for getting char to spawn at any desired spot in an aquarium, for example for making observations and for photographing.

6. Some Experiments on Visual Stimuli Releasing Digging Movements

The eye movements alone in the searching females indicated that visual stimuli are involved in the releasing mechanism of the digging movements (FABRICIUS 1953 a).

In our 1953 experiments we obtained the first clear evidence of a visual stimulation of the digging during the observations in the small filming tank. As mentioned, a female dug on a patch of sand in an enclosure, in which the rest of the bottom was covered by flat stones. The digging took a very long time, and the spawning acts which finally were seen were of a low intensity. A heap of coarse gravel had, by accident, been left behind one of the glass walls which screened off the enclosure. Now and then the female interrupted her digging in the sand, swam to the glass wall and attempted to pass through it to the gravel heap. After having observed this behaviour, we removed the glass wall. Followed by the male, the female darted to the gravel heap. There she made one single digging flap, which immediately was followed by a mating act of the highest intensity, and then she dug and spawned on the gravel in a normal way.

After this experience we made a series of experiments in which the bottom was covered by a horizontal glass plate. The first of these experiments was made in section I of the big tank. This section, which was the one with fine sand and *Isoetes* plants, was temporarily screened off from the rest of the tank by a glass wall. We dug a small pit in the sand, close to the front pane. The pit was filled with coarse »walnut»-gravel, so that the surface of the gravel reached the same horizontal level as the sand bottom, and a glass plate was laid over the gravel, covering it and a part of the surrounding sand bottom. The size of the gravel patch, which was square in shape, was 20×30 cm.

A searching female was introduced into the enclosure. She swam about in the searching manner until she happened to pass over the glass-covered gravel

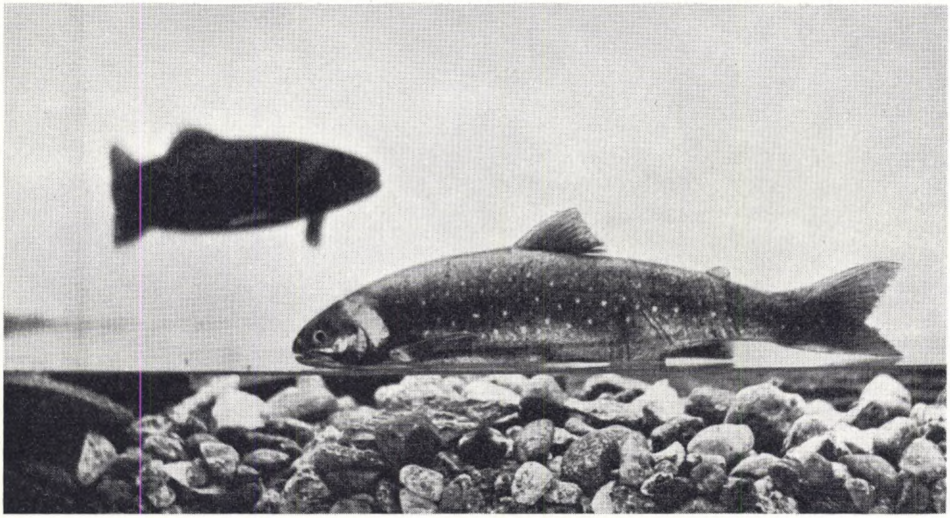

Fig. 4. Female char »searching» on a glass plate, covering a patch of coarse gravel. — Photo: K.-J. GUSTAFSON.

patch. There her searching became very intense. She remained in this part of the enclosure and turned her eyes downward every time she passed over the gravel. After 20 minutes she began »digging» on the glass plate with quite normal digging movements. Both the »sweeping» and the common digging were performed. She dug only on the part of the plate under which the gravel was visible. When she swam forward after a digging act, making a turn and returning to the plate, she never started a new digging action until her head was over the gravel, but at this moment her tail could sometimes still be on the part of the plate which covered the sand surrounding the gravel patch.

Similar experiments were made in the small photographing tank. The patch of gravel and a part of the surrounding flat stones were covered by a glass plate. Two females were studied. The first of them began digging 2 and the second one 4 $^1/_2$ hours after they had been introduced. Neither of the females dug on the flat stones, though some of these were not covered by glass. Both of them dug only on the glass plate, and only on the part of it under which the gravel was visible. When they moved in the searching on the plate they kept over the gravel, turning every time they reached the part of the glass under which the border line between the gravel and the surrounding flat stones was visible.

The movements of the »digging» females on the plate did not differ from normal digging movements (fig. 6), but one had the impression that their searching behaviour was more intense than on an uncovered bottom. This can be seen when one compares fig. 4 with fig. 1.

The fact, that female char on a smooth glass plate only dig on those parts

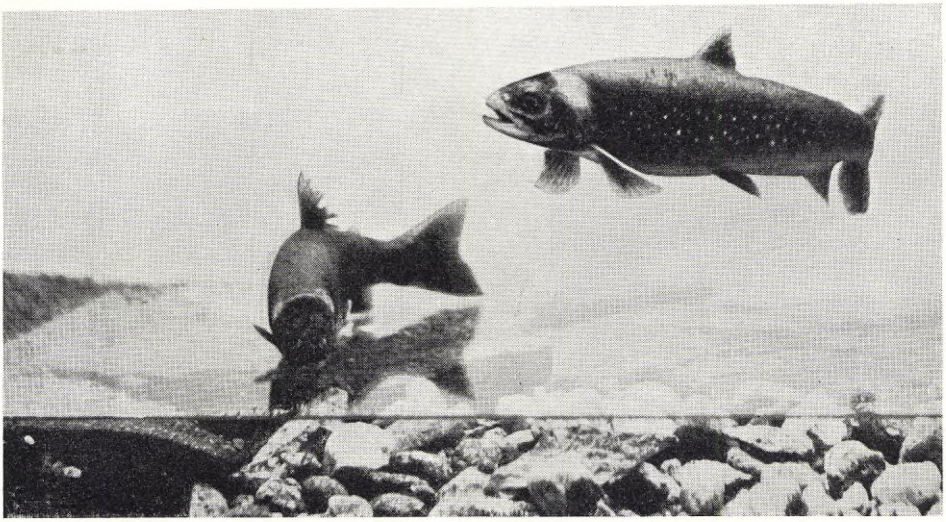

Fig. 5. A searching female turning when reaching the part of the glass under which the border line between the gravel and the surrounding flat stones is visible. — Photo: K.-J. GUSTAFSON.

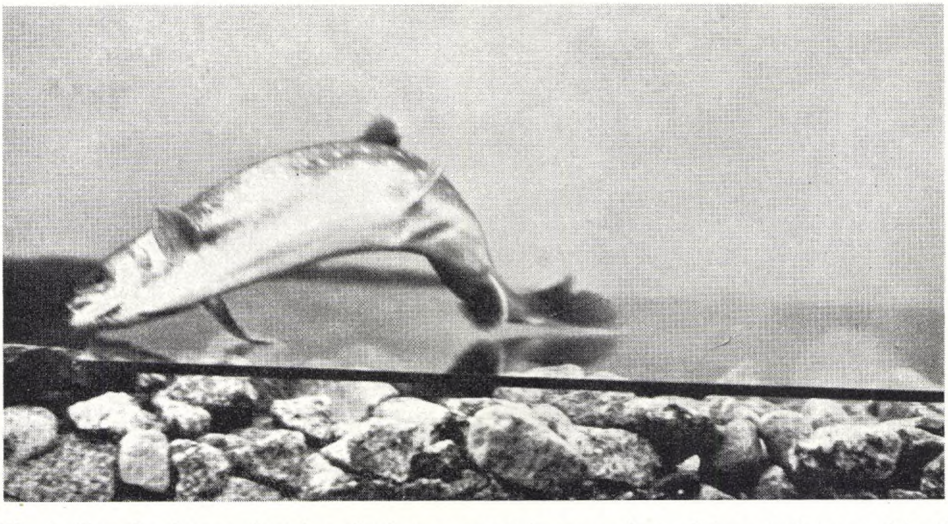

Fig. 6. Female char performing digging movements on a glass plate covering a patch of gravel. Compare with fig. 3! — Photo: K.-J. GUSTAFSON.

of the plate under which gravel of a certain kind is visible, clearly shows that the digging movements can be released by specific visual stimuli.

All the three females, which dug on glass plates, also spawned and »covered the eggs» on the glass, as will be described on pp. 82, 83 and 85.

7. Courting

For a detailed description of the courting, the reader is referred to one of our previous papers (FABRICIUS 1953 a). A characteristic feature of the courting is the trembling, shuddering or quivering movement. In our earlier experiments we got the impression that in this movement the fore part of the body swings laterally, from side to side, with very great frequency but with small amplitude, and that the axis of this movement runs approximately through the dorsal fin.

An analysis of slow-motion shots from the 1953 ciné film showed, however, that this movement is actually a sigmoid, undulating one, in which waves of lateral contortions travel rapidly from the cranial to the caudal end of the body. The amplitude of the oscillations is apparently greater at the cranial than at the caudal end, which to the naked human eye gives the impression of a lateral swinging of the fore part of the body.

Many cases of homosexual courting were seen, in males as well as in females, but in the males this behaviour was not so common as in our 1951 experiments, during which no digging females were present in the tank.

We could fully confirm our earlier statement that resting char are courted more often than swimming specimens, but experiments with models did not give any clear results. The models used in studying the attacking response were sometimes courted (p. 64). A black-coloured paraffin cast of the dorsal half of a female char, placed on the sand bottom, was courted under poor light conditions, but never in full daylight. On some occasions males were seen trembling and sometimes even ejecting milt against a stone or against their own shadow on the aquarium wall.

8. Pair Formation

When a pair had been formed, the male swam incessantly in circles round the female, courting her on each round. A male, which was watched during a period of 25 minutes, performed 107 courting acts, which gives a mean value of 4.3 acts per minute. In most of the pairs this restless circling of the male round the female was continued until the female was spent, the only interruptions being for chasing intruders away, for spawning acts and for sleeping during the night. We have also seen this circling in the field, when watching char on the spawning grounds at Borghamn in Lake Vättern.

In 12 cases we could watch the pair formation from the very beginning. In 4 of them, which probably can be regarded as the most typical ones, a searching female invaded the territory of a male, showing interest in the bottom structure somewhere in this area. She was attacked by the male and made counterattacks, followed by violent fights. The male could temporarily succeed in driving the female away, but she repeatedly returned, and at last she remained in the territory, searching and eventually digging there. Between his attacks, the male occasionally began courting the female. At this stage behaviour was frequently observed, which was a mixture of courting and attack, of the type seen in our earlier experiments (FABRICIUS 1953 a, p. 28). Gradually the male showed more and more courting and less and less attacks. Finally he only courted the female, beginning his incessant circling round her, which indicated that the pair formation was completed.

In one case a male at once joined a female, which began digging in his territory, and a pair was formed without any preceding fighting.

On many occasions a searching female penetrated into the territory of a spawning couple, attempting to occupy a site for nest-digging there. As a rule she was chased away after some fights, but twice it was observed that such a female remained in the territory, now and then fighting the two members of the spawning pair. In both cases the male, when his own female was spent or almost so, abandoned her and formed a pair with the intruding female. This happened very suddenly. The male just swam up to the new female and began circling round her. Both the deserted females remained for one day in a corner of the territory, defending very aggressively the place where they had laid their last eggs, and one of them temporarily got a new male, which circled round her for about an hour, after which she was abandoned again.

Twice it was observed that a male abandoned his territory, in which no female was present, and began courting a female that was digging by herself somewhere else in the tank. She attacked him at first and some fights followed, but soon the fighting ceased and a pair was formed, the male now defending as his new territory the area where the female was digging.

Once we also observed that a male, which had not shown any territorial behaviour, began courting a digging female and, after some fights, formed a pair with her and began defending the surroundings of her nest site as a territory.

The two last cases of pair formation we studied were more complicated. In one of them a searching female invaded a male territory, the owner of which, after the usual initial fights, began courting and circling round her. The female continued her searching, but did not begin digging. A second female then penetrated into the territory and began digging there, and as this happened, the male abandoned his first female and formed a pair with the new digging one. In the other case a pair had temporarily been removed from their territory for filming. The territory was then occupied by a new male, which soon got a female in the usual way and began circling round her. At this stage the former owners of the territory were brought back. Though the old female was spent, she returned to her territory and drove the new female away, but the new male remained there and formed a pair with her. However, he soon abandoned both the spent female and the territory.

The females had always begun their searching behaviour before the process of pair formation started, and in 6 cases out of 12 they had also begun digging. Before the females, wich were digging, had got attendant males, they were repeatedly seen courting other char, males as well as females, but they were also very aggressive towards members of both sexes.

The number of pairs formed on each day of the two experiments was as follows: In the first experiment no pair was formed on the first, 2 on the second, 6 on the third, 4 on the fourth, 2 on the fifth and 2 on the sixth day, whereas in the second experiment one pair was formed on each of the first, second and third days, and 3 on the fourth day. Some of the pairs, however, kept together only for a few hours, after which they separated and new pairs were formed, which explains why the number of pairs was greater than the total number of spawning females.

Characteristic of the pair formation were the initial period of fighting, the length of which varied from 6 minutes to 12 hours (the mean of 7 timed cases was 2 hours 21 minutes), and the subsequent intense courting and circling of the male round the female. The circling is also continued on occasions, when the female moves outside the nest pit.

After this circling had begun, fighting between the two mates was rare, but it still ocurred on a few occasions. When a male returns to the nest after chasing a trespasser away, he very often makes an attack on his female. This behaviour might probably be explained as an after discharge of the nervous mechanisms underlying the aggressive activities, which had become strongly activated during the chasing of the opponent. The female often made a counterattack, and prolonged fights could follow. Sometimes the attack made by the returning male was so powerful that the female was temporarily driven off from the nest.

It seems possible that some types of behaviour, which have been interpreted by field observers as a form of courting, can actually have been attacks on the female, made by the male in connection with his defense of the territory, or fighting at early stages of pair formation. For example NEEDHAM and TAFT (1934) when describing the activities of the male steelhead trout write: »The male, in returning to the nest from an attack on smaller fish, will often be seen to rub his nose both over and under the tail of the female as in an attempt at stimulation». (NEEDHAM and TAFT op.cit., p. 334). Also in the lake trout, *Cristivomer namaycush,* field observers have interpreted it as a form of courtship when they have seen a male nudging a female in the side (ROYCE 1951).

Another type of disturbance was also observed in the pairs. When the female moves in the nest pit while searching and digging, her red belly is more or less hidden. But now and then some of the females swam up to the water surface for air snapping, displaying their red bellies, and on these occasions they were violently attacked by their males.

In the males, the pair formation much increased their pugnacity towards other males. This was clearly demonstrated when we made cinematographic records of the territory defense. When a pair was spawning in the photographing tank, we introduced other males, taken from the big tank. All these fish were attacked by the resident male, and often by the female as well.

If the fish introduced was a male, which did not posses a territory, he almost always fled at the first attack. Territorial but unpaired males could make a few counterattacks, but soon fled. If the specimen introduced was the male member of a well-established pair, however, the result was a furious fight, which could go on for hours. The intruder could temporarily retreat to a corner, but repeatedly made new attacks, until it finally had to give up. In these fights the most beautiful mutual lateral display could be seen, in which the two males orientated themselves so that the flank was turned towards the opponent.

The pugnacity of the paired males was quite a remarkable fact, when one takes into consideration that they were not in their own territories, that their own partners were not present, and that they had just been lifted in a net from one tank to another, where they were at once attacked. It can be mentioned that BOYD (1953) has shown that in wild whitefronted geese, *Anser albifrons,* members of pairs and family groups are more successful in hostile encounters than single specimens.

If a pair were temporarily removed from their nest, both fish in most cases returned to the place as soon as they were again released in the tank. The longest absence, which was followed by an immediate return to the nest site as soon as the fish got free access to it, was 24 hours.

LORENZ (1935) has described 3 main types of pair formation in vertebrates. These types have, however, been severely criticized by BAERENDS (1950), who has suggested a more complicated classification. Further work on the patterns of pair formation in animals is apparently needed, and it would thus be premature to try to classify the char under one of the types suggested by these authors. The pattern of pair formation in the char has, however, striking similarities with that of the sticklebacks and of many birds, where the males take territories in which females are accepted after an initial period of fighting.

9. Colour Changes at Pair Formation

In the reproductive markings of the char, the brilliant red of the belly and fins does not change during the spawning period, but the dark pigment cells of the head, back and flanks seem to be under a nervous control. These parts can become darker or lighter, depending on the light conditions in the

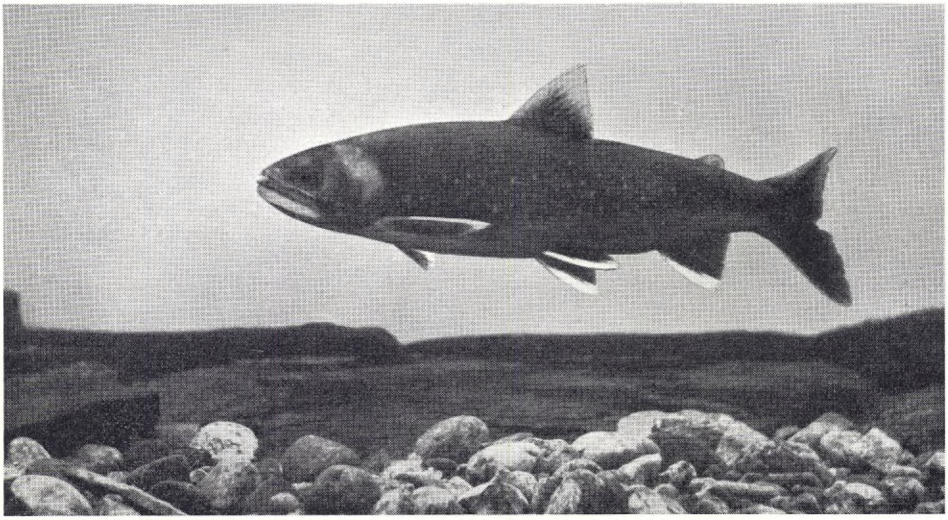

Fig. 7. An unpaired male char patrolling in his territory. The dark colouration of the back and flanks is rather uniform. — Photo: K.-J. GUSTAFSON.

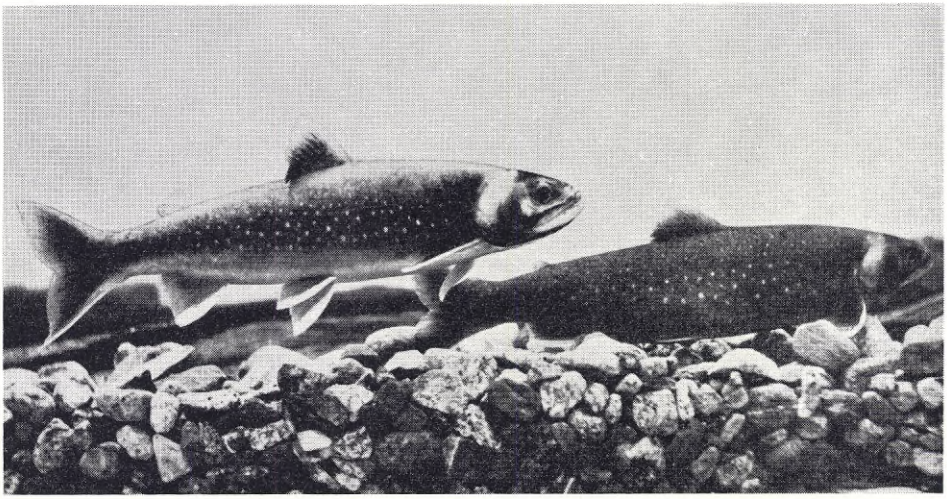

Fig. 8. The same male as in fig. 7, photographed about 30 minutes after he has begun circling round a female. The concentration of the dark colour in a strip on the flank can be distinctly seen. The female is more uniform dark. — Photo: K.-J. GUSTAFSON.

environment where the fish for the moment dwells (FABRICIUS 1953 d), and at the pair formation their pattern of colouration undergoes a remarkable change.

When a male begins circling round a female, the dark colour concentrates in a longitudinal strip about 2 cm broad on the flank, and a transversal strip about 1 cm broad on the top of the head, crossing the forehead between the eyes. The rest of the head and the back become so light that in some specimens they look almost white, with a slight tint of a metallic blue. The dark strip on the flank borders dorsally upon the lateral line, and ventrally upon the red colour of the belly. It has been observed by ROYCE (1951) that the males of the lake trout, *Cristivomer namaycush,* undergoe very similar colour changes when they begin courting the females.

These colour changes, which are demonstrated in fig. 7 and 8, occurred, more or less markedly, in all those males which formed pairs with females, and they were observed in one of the females as well. This particular female can be seen in fig 9. The interval between the completion of the pair formation and the full development of these nuptial colours in the males was about 17 to 55 minutes.

Sudden changes of colour patterns at pair formation are known to occur in some other species of fish as well, for example in cichlids (BAERENDS 1950) and in the female of *Betta splendens* (LISSMANN 1932).

10. The Spawning Act

The interval between the completion of the pair formation and the first spawning act was a rule a few hours. In 7 timed cases it varied from 37 minutes to 5 hours 36 minutes, the average being 3 hours 6 minutes.

About 100 spawning acts were watched under good light conditions. As mentioned, the female returns to the nest after every digging act, swimming in the searching manner with her tail slowly swinging laterally and her anal fin dragging on the ground like a ratchet. When she begins to be ready for mating, one can gradually see a slight change in this behaviour. When moving towards the centre of the pit, she begins to keep the anal fin constantly erected. Repeatedly and with increasing intensity courted by the circling male, she swims slowly over the ground, lowering this erected fin down into spaces between the stones at the bottom of the pit and moving forwards until the fin stops against a stone or gets jammed in a narrow crack. »Anchored» in this way by the anal fin, she bends her body backwards and performs the same trembling movement as in the courting act, and she often opens her mouth as well.

The anchoring is most probably the signal which the female gives when she is ready to spawn. As a rule the backward bending of the body results in an erection of the fore part of the fish, while its hind part rests on the ground (fig. 9—10), but sometimes it was also seen that the fore part of the females body rested on the ground and her tail was lifted instead, like in the atlantic salmon (JONES and KING 1949, 1950). Signal movements made by the female when she is ready to spawn have been described in some other

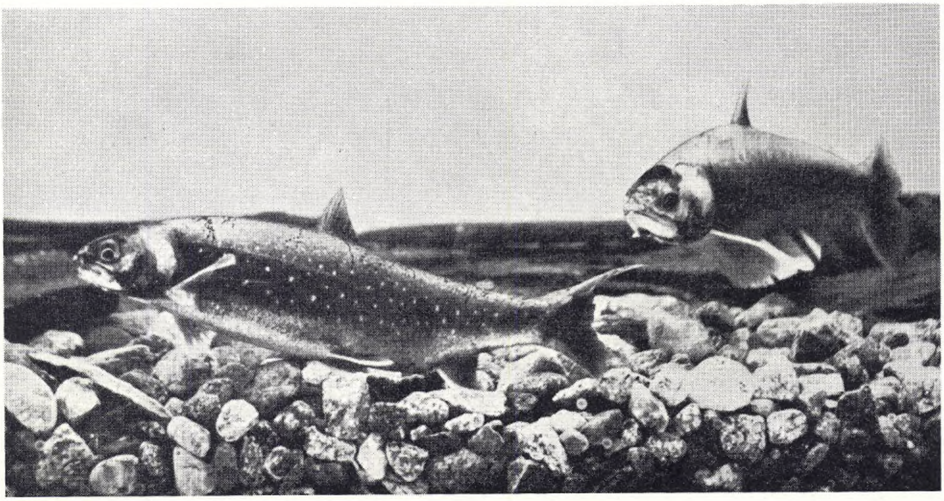

Fig. 9. Female char »anchored» in the signal posture which she shows when ready to spawn. The erected anal fin is lowered into a crevice, and the fore part of the body is raised. In this particular case the action was of a low intensity, and the female did not open her mouth. — Photo: K.-J. GUSTAFSON.

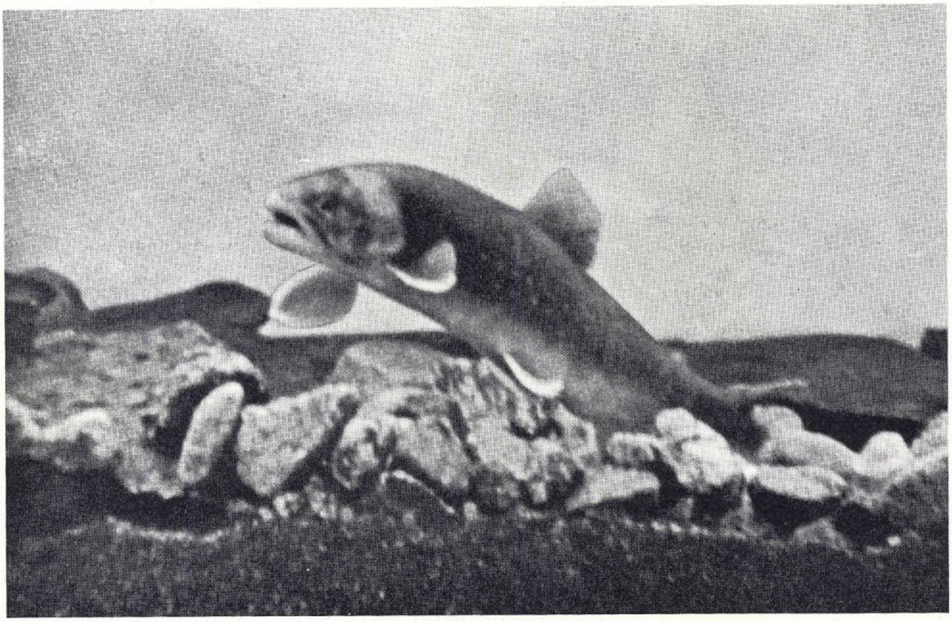

Fig. 10. Female char opening her mouth in a higher intensity degree of the anchoring action. Still photograph from the 1953 ciné film. — Photo: K.-J. GUSTAFSON.

Fig. 11. A pair of char performing the mating act. — Photo: K.-J. GUSTAFSON.

species of fish as well, for example in *Salmo salar* (JONES and KING, op.cit.), *Gasterosteus aculeatus* (TER PELKWIJK and TINBERGEN 1937), *Pygosteus pungitius* (MORRIS 1952) and *Gobius microps* (NYMAN 1953).

The first times the anchoring is performed, it is followed by a normal digging act, even if the male courts the female. The male constantly circles round the female, and sooner or later a spawning act follows when he courts her just at the moment of anchoring. He approaches the anchored female from behind and glides trembling along her side, but instead of swimming on forwards as in normal courting, he stops or at least swims very slowly when his anal fin comes close by hers. At this moment he bends his body backwards, trembles vigorously and opens his mouth wide, and both fish simultaneously expel a portion of their sexual products, as seen in fig. 11. The eggs are flung backwards in a cloud of sperm. In most cases one could see the sperm drifting over the bottom like a thin mist (fig. 12), and this was recorded in some of the ciné film shots, but under unfavourable light conditions the sperm was not visible.

Continuing the ejection of sexual products both fish start at this moment to swim rapidly forwards across the nest side by side. As the velocity of the male is greater than that of the female, the result is that she is left behind while he swims forward and upward (fig. 12).

The eggs are ejected in about 1 to 5 seconds, and the whole spawning act is over in less than 10 seconds.

Before a complete spawning act, one could in most cases see 1 to 4, or sometimes more, incomplete acts, in which the fish behaved as described above,

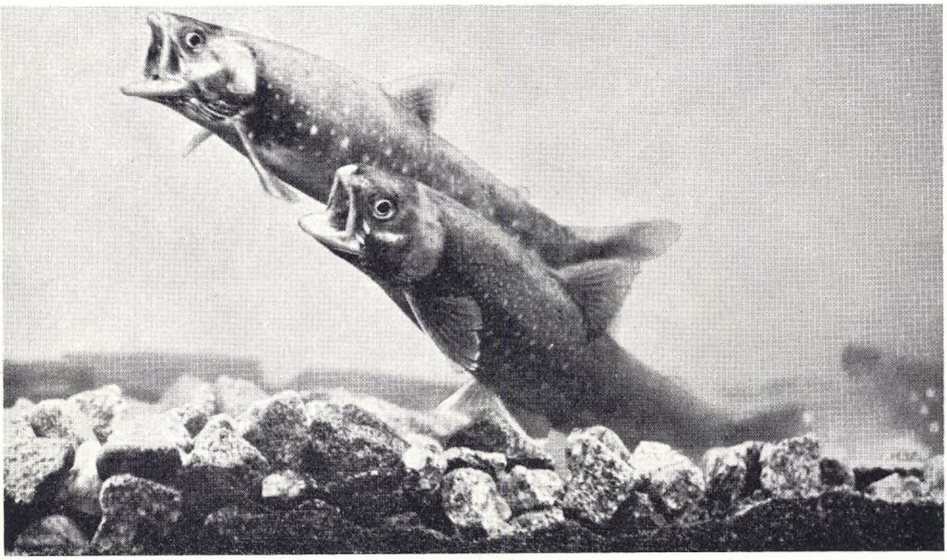

Fig. 12. Male char leaving the female behind him in the swimming across the nest which characterizes the final phase of the mating act. — Photo: K.-J. GUSTAFSON.

except that no sexual products were ejected. Sometimes such incomplete acts were followed by a period of digging, and the fish did not spawn until after a new series of incomplete spawning acts. One got the impression that the fish had to increase the intensity of their spawning behaviour gradually until it became complete. As has been pointed out by TINBERGEN (1951, 1952) and others, instinctive activities may be seen in numerous degrees of intensity, which can be arranged in a sliding scale from full intensity down to an almost imperceptible indication of it. Incompleteness occurs at a low intensity level of stimulation, and the completeness of the movement then increases with the increasing intensity of the drive. In the char this has been demonstrated in the different intensity degrees of courting (FABRICIUS 1953 a).

Some interesting observations were made in the experiments in which females »dug» on glass plates. Males were then introduced into the tank and all three females spawned on the glass.

In the first pair 5 spawning acts were seen, but the female did not perform any normal anchoring. She just stopped in the centre of the plate and rested there, slowly swinging her tail laterally. The male performed some courting acts of a very high intensity, with trembling and gaping. At the moment the two fish in one of these acts were side by side, the orgasm at once broke out in the female, and gaping and trembling she squirted a portion of the eggs on the glass and started the forward swimming, which is characteristic of the normal spawning act. The male must have ejected sperm too, for the eggs were fertilized.

In the second pair only one spawning act was seen, and the fish behaved like the first pair, except that the female, when resting on the glass before the mating, lifted her tail like the female atlantic salmon in her signal movement. Neither of these two females showed the trembling movement before spawning. In these two experiments the glass plate was so big that it covered not only the gravel patch, but the surrounding flat stones as well.

The third pair, in which 6 spawning acts were watched, showed different behaviour. The glass plate was so small that it just covered the gravel patch (fig. 6). When swimming towards the area where the digging movements had been performed, the female stopped at the edge of the glass, performing quite a normal anchoring with her anal fin against the edge of the plate and the fore part of her body over the glass. In this posture she trembled and gaped and a normal spawning act followed, in which the eggs where squirted outside the glass.

It thus looks as if it would be necessary for a normal anchoring for the dragging erected anal fin of the female to stop against a firm obstacle. We sometimes observed that the anchoring female moved slightly backwards to dip the fin deeper into a crevice.

The number of eggs deposited was small in the first spawning acts of a pair and then in the subsequent acts it rapidly increased to a maximum, whereupon it slowly decreased, becoming small again in the very last acts. On one occasion only 3 eggs were seen in the first spawning act of a pair.

The glass plate experiments, as well as the cases of spawning in section IV of the big tank, show that the char »automatically» spawn after digging, even if no pit has been formed. Probably this sometimes happens in the field as well, in cases where char spawn on rocky bottoms where the stones are too big to be displaced by the digging movements.

Normally the orgasm was simultaneous in the male and the female, but disturbances were observed in some cases. For example, in one of the spawning acts at the edge of the glass plate, the male ejected milt and then swam forward and upward, leaving the anchored female behind him, and after a few seconds she squirted her eggs alone in a delayed orgasm. Perhaps the stimulation of the female was suboptimal when she was anchored on the edge of a glass plate. Moreover, it was sometimes observed that a male ejected milt in one of the incomplete spawning acts which preceded the complete act.

11. Covering of the Eggs and Digging of Subsequent Pits

In several other species of salmonids, the female covers the eggs by digging at the upstream edge of the pit immediately after every spawning act. This has been shown in *Salmo salar* by BELDING (1934), JONES and KING (1949,

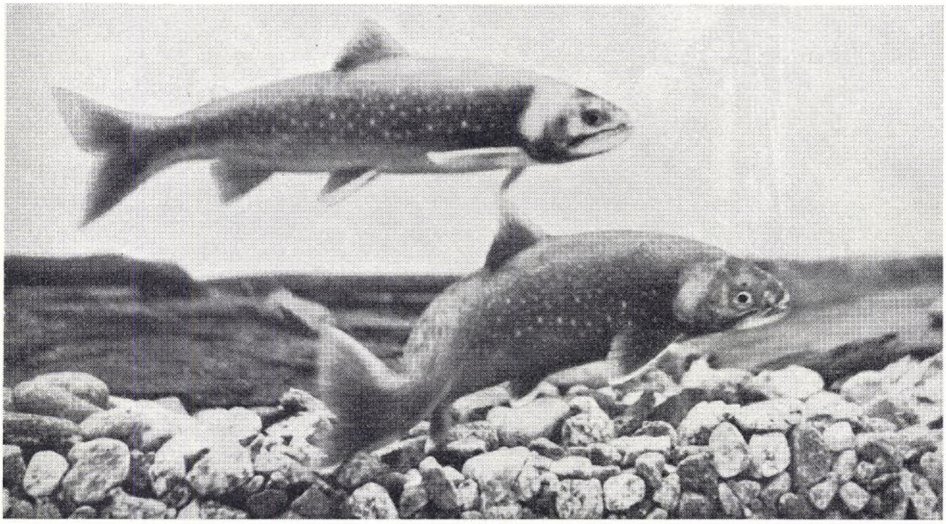

Fig. 13. Female char performing undulating movements on the gravel after spawning. This behaviour results in a sweeping down of the eggs into crevices between the stones. — Photo: E. FABRICIUS.

1950) and HULT (1950), in *S. trutta* by GREELEY (1932), in *S. gairdnerii* resp. *irideus* by GREELEY (op.cit.) as well as by NEEDHAM and TAFT (1934), in *S. clarkii* by SMITH (1941), in *Oncorhynchus nerka* by SCHULTZ and STUDENTS (1935) and by SCHULTZ (1937), and in *O. kisutch* by BRIGGS (1953).

The char seems to differ from these species by the spawning acts usually occurring in series or groups, and the covering of the eggs not beginning until after all the acts of a group have been performed. The number of spawning acts in each spell varied between 1 and 5. A series of 49 such groups gave a mean value of 1.9 acts in each. The intervals between the successive acts of a group varied from 30 seconds to 9 minutes, the mean of a series of 45 timed intervals being 2.5 minutes. The intervals between successive groups of spawning acts varied from 13 minutes to 5 $^1/_2$ hours, and the mean of 14 such timed intervals was 1 hour 55 minutes.

GREELEY (op.cit.) and HAZZARD (1932) have seen the female brook trout, *Salmo fontinalis,* covering her eggs after one single spawning act, but as this happens fairly often in the char as well, as shown by the records mentioned above, only a larger series of observations would prove an eventual difference between these two species. Apparently the char shares the grouping of the spawning acts at least with the American Dolly varden char, *S. malma,* in which NEEDHAM and VAUGHAN (1952) have seen a female beginning the covering of eggs after two successive spawning acts.

After each group of spawning acts, the female char shows peculiar behaviour in the nest. With rhytmic and rather slow snake-like undulating body movements she glides about at the bottom of the pit, sweeping the ground with her caudal, anal and pelvic fins. Contrary to her behaviour in digging, the undulating female does not turn on her side. She maintains a normal swimming posture, but her head and tail are slightly tilted down, as in the searching. These undulating movements following spawning have also been observed in the females of brook trout (GREELEY 1932, SMITH 1941) and Dolly Varden char (NEEDHAM and VAUGHAN, op.cit.), but they have not been seen in any other species of salmonid fish, though many of them have been closely studied under favourable observation conditions. Probably this undulating is an instinctive activity characteristic of the group of species which many authors regard as forming a separate genus, *Salvelinus,* to which the char, the Dolly Varden and the brook trout belong.

In all cases where the spawning had taken place on coarse gravel or rocky bottoms (sections III—V in the big tank and the gravel patch in the filming tank), the result of the undulating movements was that all those eggs, which remained on stones at the bottom of the nest after the spawning acts, were very rapidly swept down into the crevices between the stones. If, however, spawning had taken place on sand, as in section VI of the big tank and in the first experiment in the photographing tank, the eggs just rolled about in the pit and some of them could roll out of it. Only rarely was is seen that some sand or very small pebbles were slightly displaced by the gentle side to side movements of the undulating female's fins. For displacing bottom material she has more powerful movements at her disposal.

The undulating was performed by the females in the glass plate experiments as well. In the first two of these experiments the eggs rolled about on the glass when the female undulated, and within less than 40 seconds they were all swept out over the edges of the plate. She continued her undulating for some minutes even when there were no more eggs on the plate. In the third glass plate experiment the behaviour of the female was quite interesting. Though all the eggs had been squirted outside the plate, she undulated only on the glass, and only on the part of it where she had performed the digging movements.

Thus it seems as if the female when undulating would be orientated only by the sight of the bottom material in the centre of the nest and not by the sight of the eggs, though the function of the undulating movement apparently is the sweeping down of the eggs into the crevices of the nest bottom. The undulating can also be sometimes seen after incomplete spawning acts, in which no eggs have been laid.

The time the females continued their undulating, after every spell of spawning acts, varied from 1 to 48 minutes. The mean of 12 timed periods of undulating was slightly over 12 minutes. After undulating the female again begins digging, and then she usually digs on the edge of the pit. The result of this new digging largely depends on the bottom material. On the rocky bottom of section IV there was, of course, no visible result, whereas on the gravel bottoms of sections II and III the new digging resulted in stones and gravel being thrown into the nest pit, filling it up more or less completely. In one case the amount of gravel flung into a nest pit in section III was so great that, as was observed in the spawning of the Dolly Varden char by NEEDHAM and VAUGHAN (op.cit.), the nest was not only filled in but was heaped up so that a mound was formed about 5 cm high. In section V, where stones were embedded in sand, the digging resulted in sand being sucked up and flung over the place where the eggs lay in the deepened crevices. These spaces were filled with sand, which also covered most of the eggs. On the sand bottom of section VI, as well as in the first experiment in the filming tank and in our 1952 experiments, the filling up of the nest pits was very incomplete. The sand was so light that most of it was flung past the pits, and one got the impression that the females just scattered the sand about.

The fate of the eggs also depended on the bottom material. In sections III and IV, on rocks and coarse gravel, all the eggs had already been swept down into the crevices by the undulating movements of the female, and in the coarse gravel of section III the subsequent digging resulted in their being buried in the centre of the filled pit, under a layer of gravel having a depth of up to approx. 20 cm. In section V, with the stones partly embedded in sand, some eggs which lay in long crevices, parallel to the direction of the water jet caused by the digging female, were flung outside the nest. On the fine gravel and sand bottoms of sections II and VI, where the material was not permeable to the eggs, all the eggs remained visible on the bottom of the pit, after the undulating, and when the female began digging on the edge of the nest, they were almost all flung out of it and rolled about on the surrounding bottom area. Only a small number of eggs, which came to rest on the periphery of the pit, were buried by sand and gravel. This was probably why in our 1952 experiments most of the buried eggs were found in the areas which had formed the periphery of the pits.

Like the atlantic salmon, the female char, when digging to cover up the eggs, starts her next redd as well. The digging on the edge of the first nest is followed by new spawning acts and subsequent undulating at the place where this digging has been performed, and if the bottom material is sand or gravel a new pit is also formed. After undulating in her second nest, the female again begins digging on the opposite edge of it, filling it up and making her third nest, and so on.

When spawning in running water female salmonids, after having spawned in their first nest, as has been shown by JONES and KING (1949, 1950) and others, generally move upstream when making the subsequent nests. As there was no current in our tanks, the females were seen digging their second pit in any direction from the first one. It was however observed that they made their digging movements with the tail pointing towards the centre of the preceding pit, when digging a new one. Moreover, the females, after digging their second pit, dug the third and subsequent ones in the same direction, so that all the nests of a female formed a row. Only if an obstacle was encountered, was the direction changed. For example, a female in section III after having dug her first nest at the front pane, in the left part of the section, dug her next two pits in a direction straight towards the rear wall of the tank, but as the wall stopped her, she turned right, digging her fourth, fifth and sixth nests in a new row parallel to the wall.

These observations were made in the big tank. In the small gravel patch of the filming tank no rows of pits could be made. The first nest was usually made in the centre of the patch, but when digging the second one the females were already at the border between the gravel and the surrounding flat stones, and when making the third nest they again dug at the same place as their first nest. This behaviour was also shown when the gravel was covered by a glass plate, which indicates that the tendency to dig in gravel was stronger than the tendency to avoid digging at locations, where spawning had already taken place.

Several pairs of char often spawned simultaneously in different parts of the big tank, and one had to record as much as possible of what happened there. In addition, one of us had to stand in front of the small tank, operating the ciné camera. Owing to these circumstances, it was not possible to count the number of nests and spawning acts of every separate female. The largest number observed of nests made by one female was 8, but it is quite possible that some females made about 10 nests, or perhaps slightly more.

The interval between the time at which the male in the completed pair formation began his circling round the female and the time at which he abandoned the spent female varied from 4 hours to about 3 days. Observations on the 17 spawning females in the two main experiments gave a mean value of 23 hours. In seven of these fish, spawning was observed during two and in one of them during three successive days. As the fish were not active during the night, this means that the average time of effective digging and spawning activities must have been shorter than 23 hours. On the other hand, one should take into consideration that in the experiments the days were lengthened by artificial lightning which makes it probable that the period of spawning can be slightly longer in nature than it was in our experiments.

One got the impression that the spawning took a longer time in the largest females than in the smallest ones, but our observations on this point were too few to be statistically significant. It might, however, be mentioned that the female in which the shortest period of spawning, 4 hours, was recorded, was the smallest of all our females, measuring only 27.5 cm in length, whereas the female which had the longest period of spawning was one of the largest specimens, being 33 cm long. As a positive correlation between body length and number of eggs has been proved in the char (MÄÄR 1949), it seems highly probable that big specimens have a longer period of spawning than small ones.

12. Successive Polygamy

In the two main experiments 17 females spawned, but only 6 males took part in the spawning. Of these fish, 4 males and 10 females were included in the first experiment while 2 males and 7 females took part in the second experiment.

These figures express the polygamy of the males. When the female of a pair is emptied of eggs, the male often leaves her and goes through the pair formation and spawning again with a new female, which has just started her nest searching and digging. Some of these cases have already been mentioned in the chapter on pair formation. The spent females are deserted though in most cases they continue their digging and anchoring for some time.

Three males in the first experiment were polygamous, one of them spawning with 6 females in succession, which took him 7 days, and the other two spawning with 2 females, which took one of them slightly less than 4 days and the other two days. The fourth male spawned with only one female, for 2 days, but on one occasion when he was temporarily removed from the tank, his female was engaged in a spawning act with the most polygamous male which thus, strictly speaking, spawned with 7 females. The first female of one of those males, which spawned with two females, was taken over by him from the »great polygamist», which had deserted her for a new one when she was almost spent, and then her second male also deserted her, when she was totally spent, to take his second female. In the second experiment both males were polygamous, one of them spawning with 3 and the other with 4 females in succession, which took them 2 $^1/_2$ resp. 5 $^1/_2$ days.

Cases where one male has spawned with several successive females have been observed in the atlantic salmon as well (JONES and KING 1950, HULT 1950), and such a successive polygamy in the males is known in some species of birds too, for example in wrens and flycatchers (cf. VON HAARTMAN 1951 and references in this paper). Many field observers have reported polygamy in nest-digging species of salmonid fish, but in these cases they have seen one female attended by several successive males, as has been described for example by HAZZARD (1932) and by BELDING (1934).

As long as the fish are not disturbed, a polygamy of this last-mentioned type would hardly be possible in the char, because the highly pugnacious paired males are very well able to keep intruders away from their territories. It was observed that even if as many as 12 other char simultaneously invaded the territory of a spawning pair, the male soon had driven them all away by attacking them one after another, though if often resulted in his temporarily driving his own female from her nest as well. When timing the activities of such a male, we recorded 38 attacks within 25 minutes, which gives an average of 1.5 attacks per minute.

The cases of polygamy would probably not have been so numerous, if bottom material of the type most favoured for nest-digging had been present in all the sections of the big tank. Actually the section with this material was smaller than the minimum size of a territory, and consequently only one female could spawn there at a time. During the spawning of a pair of char in this zone several other females, as has already been mentioned, repeatedly attempted to invade the zone and begin digging there, but they were always attacked by the spawning pair and driven away. Not until the spawning female was almost emptied of eggs, could a new female manage to establish herself in the zone and dig a nest there, and the male in this territory often abandoned his first female then and began spawning with the new one. The fact that the section with coarse gravel was smaller than the minimum size of a territory might have influenced the choice of nest sites by the females (chapter 5) as well. But as regards the polygamy, one should also take into consideration that the occurrence of this behaviour was, on the other hand, to some extent counteracted by the cirumstance that some of the pairs were removed for fairly long periods from the big tank and kept in the filming tank where, as a rule, not more than one female was present at a time.

13. Egg-eating

Owing to the fact that 9 females in succession spawned in section III of the big tank, and that the gravel patch in the filming tank was so small that subsequent nests often were made at a place where spawning had already occurred, it frequently happened that a female dug at a location where some eggs, either her own or from another female, were already buried.

In such cases eggs were sucked up by the digging movements and flung behind the female. In the beginning of the spawning the fish did not pay any attention to these eggs, but later on they were eaten. For example the most polygamous male, which had not eaten any eggs while spawning with his first five females, began to do so when spawning with the sixth and last. He swam behind the digging female, snapping up every egg which was flung up. In spent fishes egg-eating always occurred, in males as well as in females (fig. 14.), and they were seen searching along the whole bottom for eggs. All the eggs, which had remained visible on the impermeable bottoms of sections II and VI, were soon consumed by these fish. Females, which continued digging for some time after spawning, were seen performing a digging act and then making a sudden turn, swallowing the eggs which had been flúng up,

Fig. 14. Male char eating eggs after the spawning. — Photo: K.-J. GUSTAFSON.

though these same females defended their nest sites very aggressively. Thus the char, though it also »guards» its eggs in defending the nest site, eagerly eats its own eggs as soon as it gets an opportunity to do so. When fishing one very often finds eggs in the stomachs of spawning char, which have probably been eaten under circumstances like those described above.

14. Postspawning Behaviour

After spawning the females, as already mentioned, could continue digging, anchoring, undulating and defending their territories for some time, even if they had no male in attendance. Such females also courted other char, males as well as females. Digging, anchoring and undulating were not continued for more than about a day after spawning, but the spent females could still remain at their last nests for two or three days, defending this area as a territory.

Nest-digging and territorial behaviour in spent females seem to be particularly common in some species of *Oncorhynchus,* as has been shown by HOBBS (1937), BRIGGS (1953) and others. The female *Oncorhynchus tschawytscha,* according to BRIGGS (op.cit.), sometimes continues nest-digging and defending a territory until as long as four weeks after spawning.

After the last females had abandoned their nest sites, no more true territorial behaviour was seen, though fighting still occurred occasionally, particularly in connection with feeding. Courting no longer occured in the females, whereas it still, as in our earlier experiments, was occasionally seen in the males for several months. The last courting act was seen on March 3rd, 1954, and it was performed by a male which had already got the silvery flanks of the nonreproductive colours.

15. On So-called False Redds

Among students of nest-digging species of salmonids, there has been some discussion on the occurrence of »false redds» (Briggs 1953), in which no eggs have ever been deposited.

In our aquarium experiments, we observed that such empty nests were formed under the following circumstances:

1. If there was no fully suitable bottom material for nest-digging in the tank. In such cases the females, as in our 1952 experiments, dug a large number of nests but spawned in only a few of them. If, however, a female which was attended by a male had once begun digging in an optimal bottom material, she almost always spawned in her first nest, and in all her subsequent nests too, until she was spent.
2. If a female was driven away from a nest, which she had begun digging within the territory of a spawning pair or of a very aggressive single male or female.
3. A female which, in the last-mentioned case, was driven away from the territory of a pair could begin digging by herself somewhere else in the tank, but when the female of this pair was spent, the single female could return to the place from which she had been driven away and form a pair with the resident male there, abandoning the nests she dug while alone.
4. There were, of course, no eggs in the nests dug by spent females.

The »trial nests» observed by Hobbs (1937) could belong to any of the first three categories, whereas the fourth category can be called »postspawning redds» (Briggs 1953).

16. An Experiment with Big Char from Lake Vättern

Two main types of char exist in Sweden, one of them called fjällröding (»mountain char»), and the other storröding (»big char»). They differ from each other mainly in body size, and though char generally grow big in lakes where they feed on smelt, whitefish and other small fish, while they are smaller in mountain lakes where no species of suitable food fish occur, the two types of char are often believed to be different races, or even subspecies.

Lake Vättern is the best known of the lakes where the »big char» occur, and they have been studied by Alm (1934, 1951). The char spawn on a number of rocky grounds in this great lake, and no migration into streams occurs. As it was felt that a comparison between the spawning behaviour of the two types of char would be of interest, some specimens of the »big char» were caught on spawning grounds at Borghamn and Omberg i Lake Vättern and were quickly carried to Drottningholm in an aerated tank, fitted into a car.

These fish, 4 males and 2 females, were released on October 25th in the big tank, from which all the other fish had been temporarily removed. After about 30 minutes two of the males began attacking each other and courting a third male, which rested on the bottom. At 10 a.m., on October 26th, it was observed that these two active males had begun defending territories. The two territories bordered on each other, covering sections II to V, and each of them had a size of roughly 2 square meters. The body length of the two territory-guarding males was 40 respectively 48 cm, whereas the two other males, which remained inactive, were 64 and 66 cm long. All the movements and postures in threatening, fighting and courting were exactly like those of the »mountain char».

No observations were made between 5.00 and 6.45 p.m., and when we returned at 6.45 p.m. a female had dug a deep pit in the coarse gravel of section III and was already spawning there with the male in whose territory she had begun digging. The body length of the female was 50 cm. The spawning of this pair continued during the whole of the next day, October 27th. On October 28th they still remained in the area where the eggs had been buried in the filled nests. The male occassionally defended the territory and the female showed the searching behaviour, though she was spent. On October 29th the female had abandoned her nest sites, and none of the males defended territories. Occasional attacks still occurred, and the males could now and then court the females or each other. The last courting act was observed on January 12th 1954.

All the movements of searching, nest-digging, anchoring, spawning and undulating were exactly like those of the »mountain char» used in the two main experiments, and no differences in behaviour could be observed between the two types of char.

17. Water Temperature and Light

The temperature in the big tank was kept at an almost constant level of 6.5° C, but on some occasions it was reduced to 3.5° C. Though the smaller tank was fitted to the cooling system in the same way as the big one, the flow of cooled water running through this small photographing tank was not sufficient to prevent a warming up of the water by the heat produced by the ten 500 watt electric bulbs used in filming. Every time these lights were switched on, a slow rise in the temperature began. After about two hours it had reached 10° C, and at this temperature level the lights as a rule were switched off until the water had been cooled down to about 6.5° again. These temperature fluctuations did not disturb the fish, as long as the temperature was kept below about 13° C, but at higher temperatures the char became rather inactive. Intense spawning was observed at any temperature between 3.5° and 12.5° C.

It thus seems as if rather big temperature fluctuations in the aquarium would not disturb the spawning, provided that the fish is already in a spawning condition when it is introduced into the tank. In aquarium experiments we have had similar results with other species of fish as well, for example with pike, roach, perch and burbot. The great influence of the temperature on the spawning, which can clearly be observed in the field (cf. FABRICIUS 1950 and others) probably mainly affects the time for the ripening of the gonads and the migration to the spawning grounds, whereas temperature fluctuations do not have any great influence when the spawning has already begun. It should, however, be mentioned that no statistical comparison was made of the intensity and frequency of the spawning activities at different temperatures, and thus one cannot deny the possibility that minor influences of temperature may also exist after the beginning of the spawning.

The observation tank got daylight from a row of windows in the opposite wall of the aquarium building. The char were inactive during the night, but the spawning activity began very early in the morning, about 5 a.m., when the visibility was still very poor to the human eye. In the evenings they were still active at about 6 p.m., when it was already almost dark, but at 7 p.m. the nightly resting period usually began if no lights were switched on. During the first experiment a row of six 60 watt lights were switched on over the tank every evening at about 5 p.m., and this artificial lengthening of the day caused the char to continue their spawning activity until the lights were switched off, which usually happened at about midnight.

Under these circumstances 8 spawning acts were seen between 6 a.m. and noon, 18 between noon and 6 p.m., and 47 between 6 p.m. and midnight. The high number of spawning acts observed during the evening hours is probably only due to the fact that at this time we were least disturbed and consequently were able to make more continuos observations than during the rest of the day.

During the filming it was found that the intense light of the ten bulbs, totalling 5000 watts, did not disturb the spawning fish, though these bulbs were fitted close over the photographing tank.

All these observations indicate that the char spawn in daylight, though the spawning begins early in the morning and is continued until late in the evening, in rather poor light. Actually we have seen in Lake Ransaren, as well as in Lake Vättern, spawning char on shallow grounds in bright daylight. In the last-mentioned lake there has, since olden times, been a method of fishing spawning char which is based on the fact that the spawning takes place in daylight. The fishermen row in a boat over the shallow spawning grounds, looking into the water until they discover a spawning pair of char. The spawners are easy to see, because the bright withe anterior margins of the male's fins are very conspicuous when he circles round his female. After discovering such a pair, the men lay a net round them, at some distance from the fish, and drive them towards this net by rowing inside it and splashing with their oars.

18. Filming and Photographing

The arrangement of the bottom material in the photographing tank and the strength of the lights used has already been described, and the measurements of this tank have been given. Only a few details remain to be described about the technique we used in photographing and filming.

When it was observed that a pair had been formed in the big tank, the fish were caught in a net and lifted over to the photographing tank. As a rule this treatment did not disturb the fish. After about ten minutes the male recommenced his circling and the female her digging, and the pair spawned in front of the camera. After spawning the fish were brought back to the big tank and a new pair from this aquarium were introduced into the filming tank, and so on.

In this way K.-J. Gustafson made a number of still photographs as well as a 16 mm coloured ciné film. This film shows threatening, fighting, courting, pair formation, the two types of nest-digging, anchoring, spawning, undulating, and finally some of the experiments in which the bottom was partly covered by glass plates. Most of the activities of the spawning char are shown in slowmotion shots as well as at a normal speed.

19. Discussion

All the spawning activities and their releasing mechanisms co-operate in serving the propagation of the species. The territorial behaviour leads to a spreading out of the fish over the spawning grounds, which reduces the damage done by egg predators and makes it less probable that the females dig at places, where fertilized eggs have already been buried. In the males the selection of the territory site must be governed by a releasing mechanism reacting to a certain set of stimuli, though this mechanism probably is less specialized than the mechanism for the selection of the nest site in the females. Male territories existed in all parts of the big tank, also on bottoms where the females never dug nests, but in both experiments the very first male territories were established in sections III and IV, that is to say in the areas with coarse gravel or rocky bottoms.

The territories are defended by threatening and fighting, and this aggressive behaviour is released by a mechanism reacting to several stimuli, one of which is the sight of the red colour in the spawning attire of the char. The significance of the fact that this red colour is concentrated to the under parts of the body has been discussed in our earlier papers. It has already been mentioned that the red colour is not the only stimulus to which the releasing mechanism of the aggressive behaviour reacts. Aggressive char attack moving objects of other colours as well, and therefore fish of other species than char are also driven away by the territory owners. In aquaria we have seen territory-guarding char attacking brown trout, whitefish and burbot, all of which species occur as egg predators on spawning grounds of Swedish char. Thus the aggressive behaviour apparently has the double function of keeping the territory free from other char and protecting the eggs against predators. The atlantic salmon is also aggressive to egg predators. HULT (1950) has observed spawning salmon attacking brown trout, which approached the salmon nests.

As has been pointed out by HOBBS (1937), the optimal spawning site for salmonid fish is a place where the bottom material is permeable to the eggs, and our experiments clearly showed that a successful burial of the eggs was possible only in such a material. It has been observed that some species of salmonid fish, for example the brook trout, spawn at places where there is seepage through in the bottom material (WHITE 1930, GREELEY 1932, HAZZARD 1932), and in the case of the steelhead trout (NEEDHAM and TAFT 1934) and the brown trout (STUART 1953 a, b) it has been supposed that the very occurrence of the seepage attracts the spawning fish to such places. The experiments with the char, and particularly the glass plate experiments, show that in this species the females can also be attracted to places with permeable bottom material by visual stimuli only, even if there is no seepage. Seepage, of course, occurs at many places where the bottom material is permeable, but it is probably not the most important factor in attracting the searching females. The observation made by HOBBS (1940) that in brown- and steelhead trout the state of the immediate surface material, rather than of the underlying material, decides whether or not a bottom area will be used for nesting, points to the possibility that, in these species too, the choice of nest sites is governed by visual stimuli rather than by the occurrence of seepage.

One of the most important functions of the nest-digging movements is probably to increase the permeability of the bottom material, by sucking up and flinging away the loose material in which the stones are embedded. Thus, one could say that the deposition of the eggs in a permeable material is secured both by a mechanism leading the female to a place where the bottom has this character, and by instinctive movements which further increase the permeability of the material at the chosen nest site. The anchoring also co-operates in securing the deposition of the eggs in a permeable material, for this act, which immediately precedes the egg-laying, can be performed only at a place where the crevices are so deep that the anal fin of the female can sink down in them. The permeability of the bottom substrate in the nest facilitates the burial of the eggs and secures a good oxygen supply for them. In our experiments it was observed that almost all the eggs which were embedded in sand died, whereas young char hatched from most of those buried in gravel or in crevices between rocks.

The searching in the females is an appetitive behaviour for nest-digging, but when the female moves close to the ground in the searching posture, with her head and tail bent downward, she also more or less hides her red belly, thereby reducing the possibility that the males would attack her instead of courting her. Actually it was evident that females were courted more often when searching than when just resting.

In females, which were courted by males, we could not see in our earlier experiments any immediate effect of the courting. In the 1953 experiments it was, however, evident that the courting stimulated the nest-digging movements. Repeatedly it was observed that searching females started digging when some male began courting them, and many females ceased digging, at least for some time, if their attendant male was removed. Further, a high intensity courting could release the orgasm in females. Probably the courting activates the whole reproductive instinct in the females, including the digging movements.

In the release of courting, the optimal stimulus situation must probably be the sight of the anchoring female, which suddenly stops at the bottom of the nest pit, bends her head and tail backwards, opens her mouth and trembles. This would explain why resting fish are courted more often than swimming specimens, for the situation with fish resting on the bottom contains some elements of the presumptive optimal stimulus situation. Like the anchoring female, a resting fish is close to the bottom and does not move forwards.

As has already been mentioned, the undulating movements performed by the females after spawning result in a sweeping down of the eggs into crevices at the nest bottom. The char shares this behaviour with the brook trout and the Dolly Varden char, but the undulating has not been seen in any other species of salmonid fish. One could perhaps suppose that this instinctive activity has been developed in the char as an adaptation to spawning in still water. In nests of salmonids spawning in running water, the water currents apparently often move the eggs so that they roll down into crevices. In nests of *Oncorhynchus tschawytscha* HOBBS (1937) has seen that ova circled round the basin in ever-decreasing numbers as many dropped or were carried into crevices between stones in the bottom. The brook trout, it is true, spawns as a rule running water, but it is known that this species, like the char, often spawns in lakes as well (NEEDHAM 1934, and literature cited in this paper), where the undulating certainly facilitates the burial of the eggs.

A feature characteristic of the spawning activities, as well as of all animal behaviour, is the difference in the degree of intensity and completeness at which the instinctive activities occur from time to time. In particular, this is apparent on occasions when a fish changes from one behaviour pattern to another. The spawning consists of a series of different behaviour phases, each of which is dominated by a certain type of activity. In the females the first behaviour phase is characterized by searching, the second by digging, the third by anchoring and spawning, the fourth by undulating and the fifth by digging to fill up the pit and start the next nest. At the end of each behaviour phase the intensity and completeness of the activity which has dominated this particular phase begins to decrease, and simultaneously the fish begins to show more and more elements of the activity characteristic of the next phase. Thus, the change from one behaviour phase to another is always a gradual one. When, for example, the digging is almost completed, the female begins to show more and more elements of the anchoring, as shown in fig. 2. When swimming towards the centre of the pit she begins keeping her anal fin erect and lowering it down between the stones in the way characteristic of anchoring, and soon she stops and trembles as well, but this behaviour is still followed by digging acts. It takes rather a long time until the digging activity has been completely replaced by anchoring and spawning, and sometimes it happens that outbursts of digging still remain after a spawning act. In such cases the female, when returnig to her nest after a spawning act, performs the anchoring in the centre of the nest, but this is followed by digging instead of by a second spawning act. Such an »error» is not very harmful if the spawning has taken place on a permeable bottom, but if the nest is situated in sand or fine gravel the result is destructive to the eggs, which are flung out of the pit by the »erraneous» digging movements. In the same way the undulating does not disappear suddenly. When the female has already begun digging to fill up the pit and is making her next nest, she still undulates slightly for some time every time she approaches the digging place.

Finally it should be mentioned that the spawning behaviour is not exclusively governed by inborn releasing mechanisms, reacting to sign stimuli. An important role is played by conditioned responses as well. The males must soon be conditioned to their territories and the females to their nest sites, and this conditioning apparently takes place very rapidly. Probably a rapid conditioning is also involved in the repeated digging at a certain spot which is necessary for making a pit. Moreover, the members of a well-established pair must be conditioned to each other, for they rarely fight between themselves, though they vigorously attack all other fish.

20. Summary

The spawning behaviour of the char was studied in a big tank, provided with an electric cooling system. Almost immediately after having been introduced into the aquarium, the char began threatening and attacking each other. In the threat postures the char display some details of the spawning colouration, which probably act as signals releasing flight or submissive behaviour in the opponent.

Already before any pairs had been formed, the males established and guarded well-defined territories. Four territories could exist in a tank the bottom area of which was 1×7 m, whereas in a smaller aquarium, with a bottom area of 2.2×0.6 m, one male after a series of fights became dominant and guarded the whole tank as his territory.

Experiments with cardboard models showed that aggressive char attack moving objects of almost any shape, size and colour, but red objects were attacked more frequently than models of other colours. The sight of the red colour in the spawning attire of the char is, thus, apparently one of the stimuli which release the aggressive behaviour.

A description is given of the two types of nest-digging movements which were observed in the females. Some observations were made on the effect of digging in different bottom substrates.

The selection of nest sites was studied in the big tank, where zones with different bottom material had been arranged. Most of the females preferred a coarse gravel bottom, consisting of stones roughly walnut-sized. When selecting the nest site, the female is governed by visual stimuli. This was demonstrated by a series of experiments in which the bottom was covered by a glass plate. The females performed digging movements on the plate, but only on locations where coarse gravel was visible under the glass.

Some details of the courting are described. The movement of the courting fish, which to the naked eye looks like trembling, is actually a very swift undulating.

The pair formation apparently begins in most cases with a female invading the territory of a male. She is at first attacked but soon the aggressivity in the male is replaced by courting and he begins an incessant circling round the female. The pairs usually remain together until the female is spent, and the circling of the male round the female is continued during the whole of this time. Some variations of the pair formation process are described. Colour

changes occur at the pair formation, particularly in the males. Paired males are more aggressive than unpaired ones.

When ready to spawn, the female shows a signal movement which could be called the anchoring. She suddenly stops in the centre of the nest pit, lowers her anal fin down into some crevice in the bottom, bends her body backwards, trembles and opens her mouth. The male responds by swimming up parallel to her, and both fishes swim side by side across the pit in a spawning act, squirting out their sexual products. The experiments, in which the bottom was covered by a glass plate, showed that the female char finally spawn after digging, even if no pit has been made.

After 1 to 5 successive spawning acts the female performs snake-like undulating movements in the nest. As a result of this behaviour, all the eggs are rapidly swept down into crevices in the bottom. After undulating the female begins digging again on the edge of the pit, filling it up and starting her next nest as well. Every female makes several nests and generally performs more than one spawning act in each of them.

The males showed a successive polygamy, abandoning their spent females for new ones. One male could spawn with as many as six successive females.

After spawning the females remained at their nest sites for some days, often defending this place as a territory.

An account is given of some cases in which females dug so-called false redds, where no eggs were deposited.

No differences in behaviour were found between big char from Lake Vättern and smaller char from Lake Jormvattnet.

The char were inactive at midnight. The spawning took place at daytime, and it ocurred under different light conditions, for example in poor light as well as in the very bright light of the bulbs used for photographing. In the aquarium the char spawned at any temperature between 3.5 and 12.5° C. The spawning was not disturbed by temperature fluctuations within this range.

A ciné film of the spawning of the char was made, and some details of the technique used in filming are described.

The function of the spawning activities and their releasing mechanisms are discussed, as well as the rôle of conditioning in the reproductive behaviour of the char.

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Addendum

At the same moment that this manuscript was to be sent to the printers, we received a new paper by JONES and BALL (JONES, J. W. and J. N. BALL. 1954. The Spawning Behaviour of Brown Trout and Salmon. *Brit. Journn. Anim. Behaviour* 2: 103—114).

The authors give a detailed account of the spawning behaviour of the brown trout as seen in an aquarium tank and compare it with the behaviour of the atlantic salmon, which one of them (J. W. J.) has studied for many years.

There are some striking similarities between the behaviour of the brown trout and that of the char. The posture of readiness in the female, called »anchoring» by us and »crouching» by JONES and BALL, seems to be almost identical in the two species. In fighting the char and the brown trout very often actually bite their opponents, which the salmon rarely does.

On the other hand the brown trout and the salmon share some features of behaviour in which they differ from the car. In both the first-mentioned species only one spawning act is performed in each nest, and the female starts covering up her eggs immediately after this act, whereas in the char several spawning acts can be performed in each nest, and the female always makes undulating movements before she begins covering her eggs. The type of digging movements, which we have called the »sweeping», has not been seen in salmon and trout. Gaping in courting, courting performed by females and homosexual courting seem to be more common in the char than in the other two species dealt with here.

The brown trout, finally, has some behaviour patterns of its own, in which it differs from both the salmon and the char. Whereas in salmon and char the threat display mainly consists of an erection of the fins, the brown trout has some peculiar threat postures, some details of which have been described by FABRICIUS (1953, p. 19), STUART (1953) and by JONES and BALL (op.cit.).

The authors give a detailed report on the nature and function of the trembling or quivering movement in the orgasm and courting of salmon and trout, and they endeavour to find a separate function for this movement in any particular situation in which it may occur. We do not see why this should be necessary. Under certain conditions the trembling releases the ejection of the sexual products. More or less incomplete low intensity forms of the quivering action occur as »courting», and they seem to stimulate the whole reproductive instinct, in the sense TINBERGEN (1951) has given this word. As has been observed both by JONES and BALL and by us, this courting apparently stimulates the digging movements in particular. The releasing mechanism of the courting reacts to so simple sign stimuli, however, that this action often occurs under inadequate conditions, a phenomenon which is extremely common in animal behaviour. As JONES and BALL themselves describe, male trout have been seen quivering against a wall or stone.

JONES and BALL are of the opinion that the quiver may sometimes function as a threat. If a »courted» brown trout does not respond either by moving away or starting digging movements, it is attacked by the »courting» fish. This only happens very rarely in the char, and in these few cases we think that this behaviour could be explained in another way than by assuming that the »courting» quiver is a threat. In a spawning fish both the courting drive and the fighting drive are activated, and the behaviour of the specimen is dominated sometimes by the one and sometimes by the other of these two drives. Changes from one of these behaviour patterns to the other occur particularly when the nervous mechanism underlying one of them has been

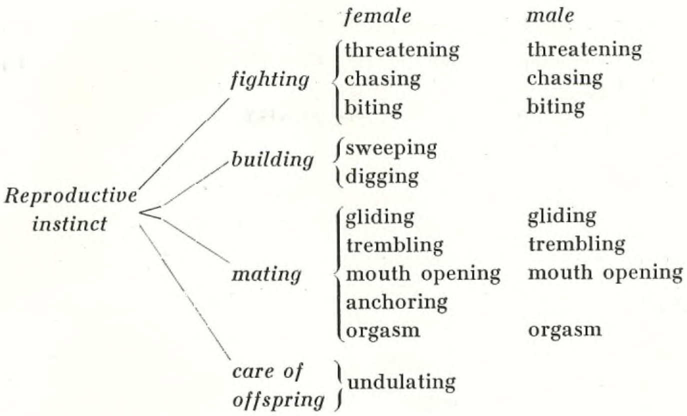

Fig. 15. Schematic drawing illustrating the probable hierarchical organization underlying the spawning behaviour in the char.

discharged for the moment (FABRICIUS 1953, p. 27—28). It would be very interesting, however, if the quiver in the brown trout really would at times act as a threat, particularly in view of the fact that we have found that there is another species of salmonid fish, viz. the grayling, *Thymallus thymallus,* in which the quiver quite definitively occurs as a part of the threat display and of the fighting (FABRICIUS and GUSTAFSON, unpubl.).

Finally, we do not fully agree with JONES and BALL's view of the hierarchical organization underlying the spawning behaviour of salmon and trout. On p. 110 they present a schematic drawing in which the major reproductive instinct has been divided into four sub-instincts, viz. courting and fighting, building, mating, and care of offspring. On the next page they say that »it is probable that the courting quiver of salmon and trout is . . . an isolated part of the male orgasm behaviour pattern curtailed because the sign stimulus releasing the rest of the pattern is not given by the female». If this is true, the courting must only be a part of the mating sub-instinct and it cannot, as shown in the above-mentioned drawing, belong to the same sub-instinct as fighting. We suppose that this error is due to a confusion between the underlying nervous mechanisms and the functions of the instinctive actions. If one would attempt to illustrate the organization of the spawning behaviour in the char in the same way as TINBERGEN (1942, 1951) has done for the three-spined stickleback, one would rather get a scheme as shown in fig. 15.

In the char the undulating of the female in the nest, resulting in a sweeping down of the eggs between the stones, is the only action which can with certainty be regarded as care of the offspring. The digging to fill up a nest, it is true, results in a covering of the eggs, but it seems doubtful whether it can be regarded as a pure »care of offspring», because it results in the formation of a new pit for the next spawning as well. Some of the different types of digging observed by JONES and KING (1950) and JONES and BALL (op.cit.) can probably be explained as different intensity degrees of the digging action.

There certainly is only one sub-instinct of fighting, which is active during the whole reproductive season, but at different stages of spawning this fighting has different results or »functions», viz. defense of the territory, defense of the female, defense of the pit where digging is performed, and defense of the eggs.

Experimental Observations on the Spawning of Whitefish, *Coregonus lavaretus* L., in the Stream Aquarium of the Hölle Laboratory at River Indalsälven

By Eric Fabricius and Arne Lindroth

1. Description of the Tank

The flowing water tank (fig. 1.) of the Hölle laboratory is 950 cm long and 190 cm wide. The depth is 130 cm at the long side facing the observation chamber, and 75 cm at the other long side, which forms the rear wall. The bottom thus slopes towards the long side facing the observation chamber, and 5 plate glass windows, each measuring 180 × 130 cm, are incorporated in this long side. Water from the river flows through the tank, passing one grating at the upstream end and another at the downstream end. The velocity and depth of the water can be regulated by a valve in the main intake tube at the upstream end, and by a sluice at the downstream end. A more detailed description of this tank has been given elsewhere by Lindroth (1954).

2. The Spawning Behaviour of the Whitefish

On December 18th, 1932, a school of spawning whitefish was observed in the Lake of Constance by Elster (1934). The fish moved at the water surface, and a pair of whitefish were seen diving down towards the bottom immediately after they had released their sexual products. The eggs slowly sank down in a cloud of sperm. A lot of splashing was observed at the water surface. The spawning act itself was not seen.

Apart from this short account, no description of the spawning behaviour of the whitefish has been published, as far as we know. Apparently the main reason for this lack of observational data has been the fact that the whitefish, as has been described by Schweizer (1893), Wagler (1941) and Toots (1949), spawn in most cases at night. Moreover, whitefish are known to be difficult to keep in aquaria.

From Sundsvall Bay, on the coast of the Baltic Sea, whitefish migrate in the autumn into the River Indalsälven, where spawning whitefish are caught by hauling nets on some stony and sandy grounds. In November 1953 two experiments were made in the Hölle laboratory with spawners caught in this fishing.

Five sections with different bottom material were arranged in the tank, each of them facing one of the front panes (fig. 1). Beginning from the upstream end, these sections were numbered I—V. In sections I, IV and V the bottom material was a mixture of larger and smaller stones, partly embedded in gravel of varying coarseness. Section II had a smooth sand bottom, whereas in section III the bottom was built up of fairly big stones, measuring about 10 to 25 cm in diameter. Because this layer of stones had been made so high that it almost reached the water surface, the stream was more swift and turbulent in this section than in the other parts of the tank, where the velocity of the flowing water was about 0.2 m a second. During the experiments the depth of water was kept at about 70 cm.

The tank obtained daylight from a row of windows over it. At the latitude of Hölle, the days are rather short in November. From about 8 a.m. there is sufficient light to permit observations, and from about 2.30 p.m. it begins to grow dark again. Writing becomes rather difficult from about 3 p.m., and after 4.30 p.m. one is no longer able to see the fish in the tank. Artificial light was, as a rule, not used, because it was found that it disturbed the fish. During the experiments, the water temperature slowly sank from 3.4 to 1.5° C.

The first experiment, with 40 whitefish, was made in the middle of November. The fish spawned, and the spawning took place late in the afternoons when it was already rather dark, but no close observations could be made. The second experiment began on November 20th, at 12 noon, when 12 male and 12 female whitefish were introduced in to the tank. The top of the dorsal fin had been cut in the males, in order to make it easier to distinguish between the sexes.

The body length of the adult whitefish was about 30 to 40 cm. Apart from the spawners, the tank contained 10 young whitefish one summer old and having a body length of about 15 cm. There was a striking difference between the behaviour of the adult and the young fish. The young whitefish formed a dense school, always following each other, whereas the adult specimens roamed about almost independent of one another. The spawners formed a school only on occasions of disturbance, for example when frightened by sudden movements outside the panes, or when a light was switched on, but they always dispersed again soon.

From November 21st to November 30th the number of adult whitefish present in each section of the tank was, as a rule, counted at least once a day. Ten such counts gave an average of 4.7 for section I, 7.1 for II, 6.7 for III, 8.4 for IV and 6.9 for V. The distribution thus seemed to be rather haphazard, but perhaps with a slight avoidance of both the ends of the tank and of the »rapids» in section III. This avoidance could well have been due to the stream

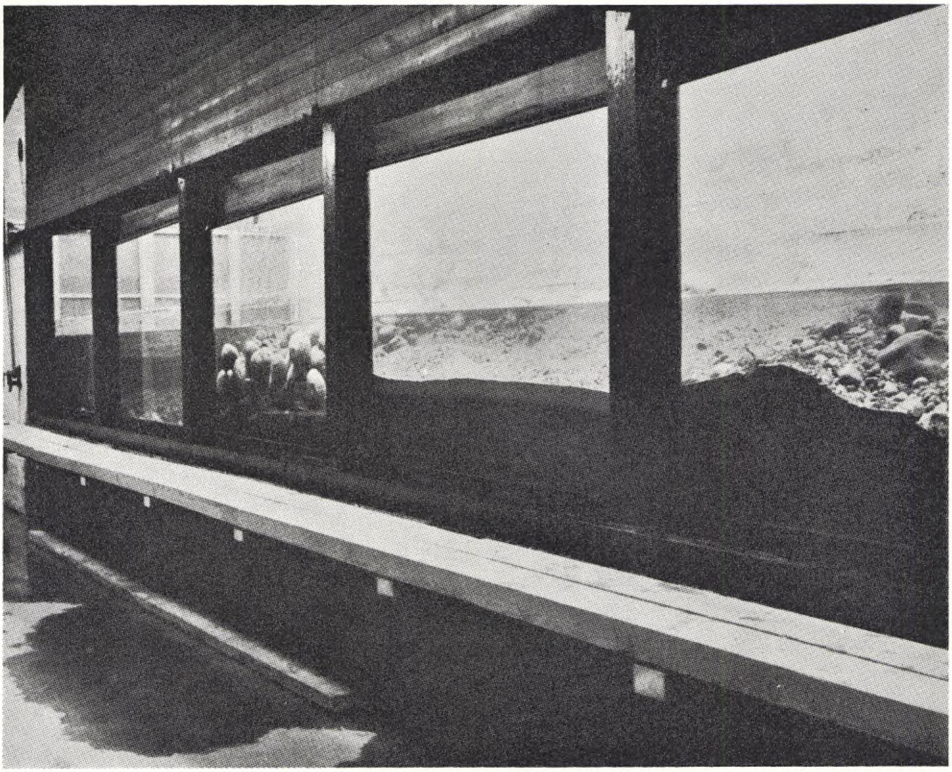

Fig. 1. The observation chamber and the tank, seen from the upstream end. Photo: B. SVENONIUS.

conditions. It should be mentioned that the water in section I was rather turbulent, because the grating at the upstream end of the tank had been partly obstructed by silt and debris, so that there was a fall of water over the top of the immersed part of that grating.

We found that the most characteristic features of the behaviour of the whitefish were that they never rested on the bottom, and that they never showed any fighting, nipping, chasing, threatening or other aggressive behaviour. Actually, the whitefish seem to be the most peaceful species of fish we have ever watched. Displacement snapping and prey-shaking (FABRICIUS 1953) were seen on some occasions. In the daytime most of the adult whitefish swam about close to the bottom, and many specimens were seen taking sand and gravel in their mouths and ejecting it again, or even actually feeding on whitefish eggs. Our observations thus confirmed the statement made by SELIGO (1908), ELSTER (op. cit.) and SEGERSTRÅLE (1947) that the whitefish do not cease feeding during the spawning season. Eggs, remaining from the spawning in the first experiment, were present in all parts of the tank, and the number of eggs increased, because eggs now and then dropped out from many of the females. This abnormal egg-dropping in captive females has been observed in the char as well (Fabricius 1935, Fabricius and Gustafson 1954), and it may be mentioned that we have found it extremely common in the grayling, *Thymallus*.

While swimming close to the bottom, some of the adult whitefish, males as well as females, adopted a posture resembling a lateral display. Slightly tilting the head and the tail down they at first erected their pelvic fins, and with increasing intensity of the action they turned the pectoral fins to their foremost position, and finally they could erect their dorsal fin as well. In this way they slowly swam about in a »sailing» manner. Some of these »sailing» fish could remain for several hours over a bottom area of only two or three square meters, but as these areas were not defended, they could not be regarded as territories in the sense in which modern ecologists use this word (cf. Howard 1920 and Tinbergen 1936, 1939).

From November 21st to November 30th a marked change in the behaviour of the fish could be observed every day at about 3 p.m., when it began to grow dark. The school of young whitefish dispersed and its former members moved about singly in all parts of the tank, feeding on eggs. The adult fish often became very lively and were seen swimming about near the water surface. Adopting the same posture as in »sailing», some specimens now and then made swift rushes towards the surface, causing a lot of splashing.

Actual spawning was observed on November 27th and 29th, at 3.25 and 4.02 p.m. respectively. As it was very difficult to see the fish in the dark, some very faint red bulbs were switched on over the tank in the afternoon of November 30th. These did not disturb the fish, and on this particular afternoon, from 3.30 to 5.30, three complete and several incomplete spawning acts were watched. In spawning a male approached a female, usually near the bottom of the tank. Side by side, touching each other's flanks and performing spasmodic undulating lateral body movements, the two fish swiftly swam obliquely towards the water surface, heading against the stream. Their fins were erect, and their bodies were slightly curved with head and tail down, as in »sailing». Though very swift, the undulating body movement did not give the same impression of a quiver as the corresponding movement of char, salmon and trout. It rather looked like stiff and »exaggerated» swimming movements. The male pushed himself against the flank of the female so powerfully that she was partly turned on her side, as seen in fig. 2. When reaching the water surface, or sometimes about ten cm below it, the two fish simultaneously released a portion of their sexual products. We estimated that 50 to 300 eggs were ejected in each spawning act. It could not be seen whether the fish opened their mouths in the orgasm or not. Immediately after the mating act the male and female separated, while the eggs sank down to the bottom. Some

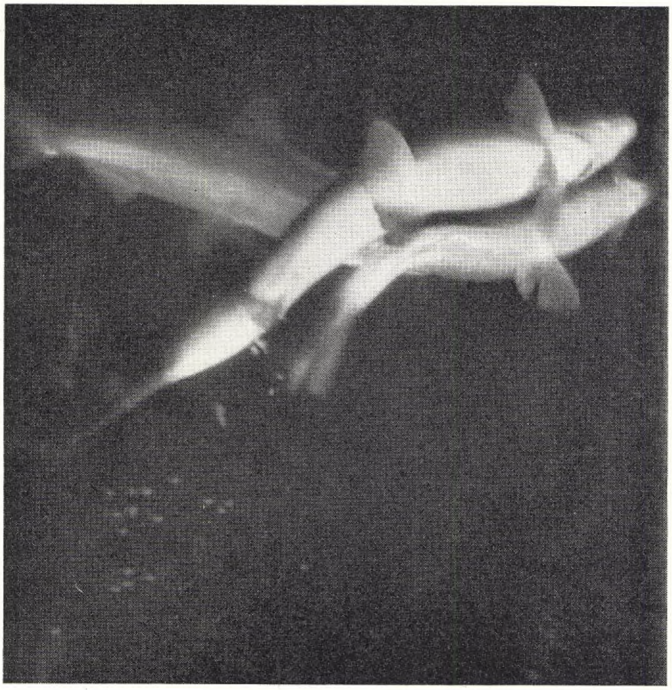

Fig. 2. A pair of spawning whitefish. The upper fish is the female. The maximal erection of the pelvic fins can be clearly seen, particularly in the male. A number of sinking eggs are visible under the tail of the female, and another whitefish is approaching the couple from behind to eat the eggs. Photo: H. PETERSON.

eggs were eaten by other whitefish before they reached the bottom, and on one occasion a pair, which had just performed a spawning act, were seen taking part in this snapping up of the sinking eggs.

The spawning whitefish showed complete promiscuity. Some minutes after spawning with one partner, a fish could be seen spawning with another partner somewhere else in the tank. A male and a female never remained together after a spawning act. They approached each other a few seconds before the act, and immediately separated again after it. Apart from the complete spawning acts, a number of incomplete acts were seen, in which two fish swam side by side to the surface, performing the same undulating movements as in spawning, but without ejecting any sexual products. Two partners involved in such an incomplete spawning act could either be of the same or of the opposite sex. The whitefish thus show a homosexual behaviour of the same type as has been observed in the char (FABRICIUS 1953, FABRICIUS and GUSTAFSON 1954). Single specimens were also seen rushing towards the surface, performing the same movements as in spawning, and this behaviour was shown by males as well as by females.

On reaching the bottom, the eggs slightly adhered to stones and pebbles. Those eggs, which remained visible on the top of stones or on the smooth sand bottom, were soon eaten by the fish, while those that sank down in the crevices survived. The young hatched in the middle of May. They immediately swam up to the water surface and were swiftly carried away by the current.

The whitefish lived in the tank the whole winter. When visiting the laboratory in March, we observed that they showed different behaviour from that shown during the spawning season. The adults and the young fish formed a mixed school, which moved about in the tank, keeping well together.

The whitefish spawn in brackish coastal areas of the sea, as well as in lakes and rivers. Though our experiments confirm the observations made by ELSTER (op. cit.), that the spawning takes place »pelagically» in the free water, it is a wellknown fact that the whitefish in many cases concentrate on certain spawning grounds, which often are characterized by a particular kind of bottom material, as has been described, for example, by JÄRVI (1928), FREIDENFELT (1934), WAGLER (1941), FABRICIUS (1950) and SVÄRDSON (1951). In our tank the whitefish did not, however show any clear preference for certain areas, and spawning was observed in all parts of it. The experiments thus failed to throw any light on the rôle of the bottom material in the spawning of the whitefish, probably because all the bottom material used in the tank was of kinds actually occurring on natural whitefish spawning grounds.

The undulating body movements of the spawning whitefish were apparently performed in almost the same way as the trembling or quivering in the spawning and courting of salmon, trout and char, which is also an undulating, though it looks like a trembling because it is so rapid. It may be mentioned that a ciné-film of the spawning behaviour of the char, made at Drottningholm in September 1953, (FABRICIUS and GUSTAFSON 1954) contains some slow-motion shots of the »trembling», in which this movement, when seen at a low speed, looks very much like the undulating of the whitefish, but the amplitude of the swinging movements is greater in the whitefish than in the char and other related salmonids. In the spawning whitefish one got the impression immediately before the orgasm, at least, that the undulating movements of the male and female were synchronized, so that the two partners »kept time and pace» in these movements.

During the spawning season the whitefish have some parallel longitudinal rows of pearl organs on the flanks. The fact that the male and the female swim side by side in the free water, touching one another's flanks and pushing themselves against each other, makes it very probable that these pearl organs, as has been supposed by WAGLER (op. cit.), have the function of helping the pair to remain in contact with each other during the spawning act by making the flanks of the fishes rough. This does not, however, exclude the possibility that these organs can have other functions as well. Their white colour makes them so conspicuous that they could easily serve as visual signals, and of course these hard organs can provide a tactile stimulation in addition, as has been supposed by NÜSSLIN (1907). In the spawning season the whitefish, apart from the development of the pearl organs, maintain their usual colours, in which the back and the fins are dark, while the flanks and the belly are silvery. On the pelvic fins, which are always erected in the act of »sailing» and in spawning, one can, however, see some rows of small brown spots and a narrow light anterior margin in living specimens.

Summary

The spawning of whitefish from the River Indalsälven was observed in a big tank with running water. All spawning took place late in the afternoon, when it was already rather dark.

In spawning a male and a female, touching each other's flanks and performing lateral undulating body movements, swam side by side up to the water surface and released a portion of their sexual products. The eggs sank down to the bottom. The whitefish did not defend territories, nor did they attack, chase or threaten each other. The spawning was quite promiscuous, every specimen spawning first with one and then with another partner. No marked schooling behaviour was shown in sexually mature fish during the spawning season, but some months after spawning the same whitefish specimens formed a dense school in the tank.

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A Stream Tank at the Hölle Laboratory[1]

By ARNE LINDROTH

The intense work which is at present being carried on in Sweden, chiefly through the Migratory Fish Committee, on the conservation of salmon, comprises fundamental research on salmon biology. The research includes field investigations and laboratory experiments on the biology of salmon parr and smolt production capacity of those rivers where salmon, now or in the nearest future, must be maintained by artificial means on account of the utilization of the rivers for hydroelectric purpose. Knowledge of the biology of young salmon — choice of bottom, inter- and intraspecific competion, holding of territories, feeding habits, reaction to environmental changes etc. — is particularly important in these investigations. Studies of this kind can only be performed in the field or in large aquaria with streaming water. Thus, JONES and KING have observed and filmed salmon spawning in an observation channel in the River Dee in Wales (JONES and KING 1949, 1950).

To enable studies along these lines on both salmon and other stream fishes, a large stream tank has been constructed at the salmon laboratory of the Migratory Fish Committee at Hölleforsen on the River Indalsälven.

The stream tank is housed in a special building, the greater part of which is under ground level, with an area of 4×16 meters (Fig. 1). It consists of an entrance chamber (A), which by means of a Thomson overflow weir (B) is separated from a forechamber (C) (see fig. 2). From here the water passes through changeable gratings (D) to the aquarium propre (E) and then through a grating (F), over stop logs, through a sluice gate (G) and out through the exit chamber (H). Along the aquarium lies the observation room (I).

The building is made of reinforced concrete. The roof is fitted with 7 pivoted windows of wire glass over the aquarium.

The aquarium (Fig. 3) is closed off from the forechamber and exit chamber by changeable gratings of brass wire nettings. Against the observation room there are five windows 180×130 cm, of 20 mm mirror glass. The putty used between the window-glass and the iron frames is plastelin. Blinds can be

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[1] Report from the Migratory Fish Committee.

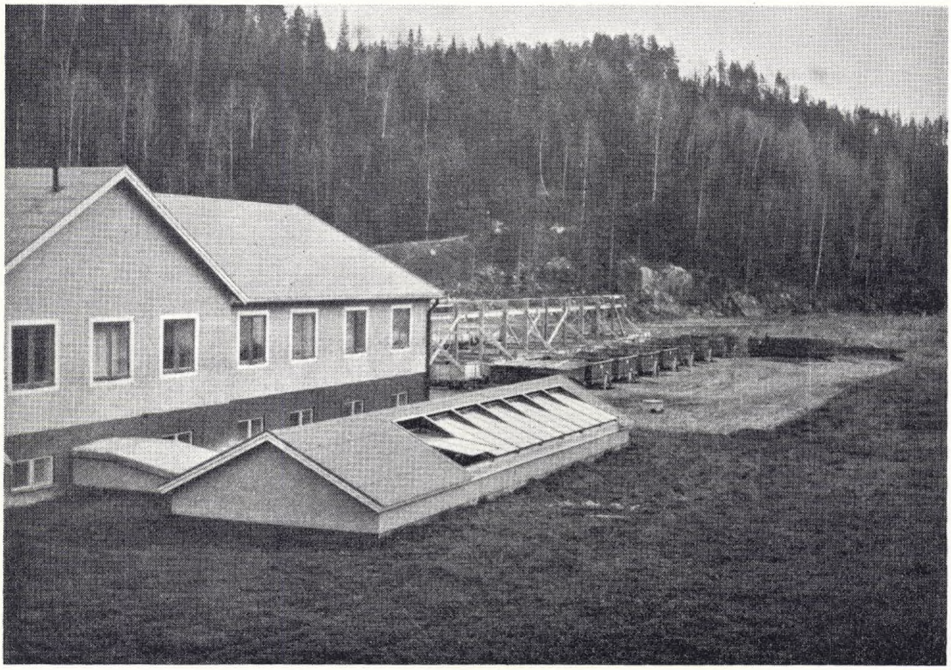

Fig. 1. The stream tank building at the Hölle laboratory (Photo: SVENONIUS).

drawn to screen off the observation room so that the observer is not unnecessarily illuminated. (See fig. 4.)

The aquarium is 950 ×190 cm and the fittings are of wood. The bottom is divided into two areas of different levels. The deeper area adjacent to the observation room is 85 cm wide. The shallow area is 55 cm higher, 105 cm wide, and slopes towards the deeper one. (See section, fig. 2.) On the boundary between these two areas the aquarium can be furnished with a longitudinal wall. Bottom material of desired composition may be laid on the two areas.

The supply of water is regulated from 0 to 1.5 m^3/sec by a sluice valve on the inlet pipe, and is read on the level pipe (K) as the level over the overflow weir. The water level in the aquarium is regulated by insertion of stop logs and by the sluice gate, from complete exposure of the wooden floor up to 130 cm above the lower bottom level. The water velocity can be varied within wide limits by changing the water supply and level.

The illumination of the aquarium consists at present of four 2 × 40 W tube bulbs.

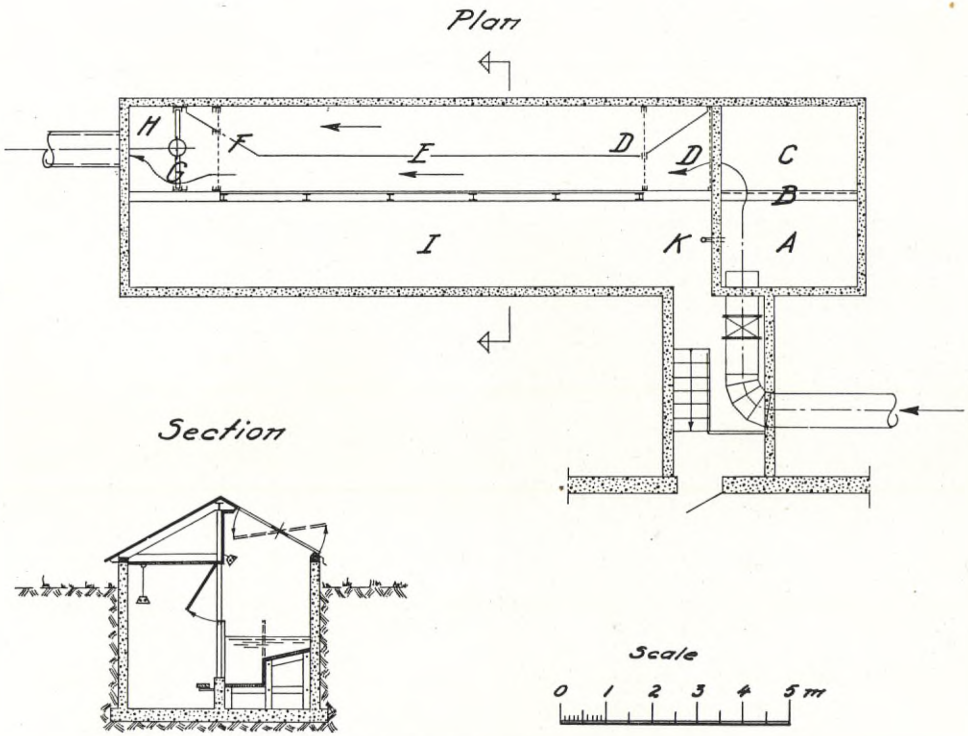

Fig. 2. Plan and section of building. For description see text.

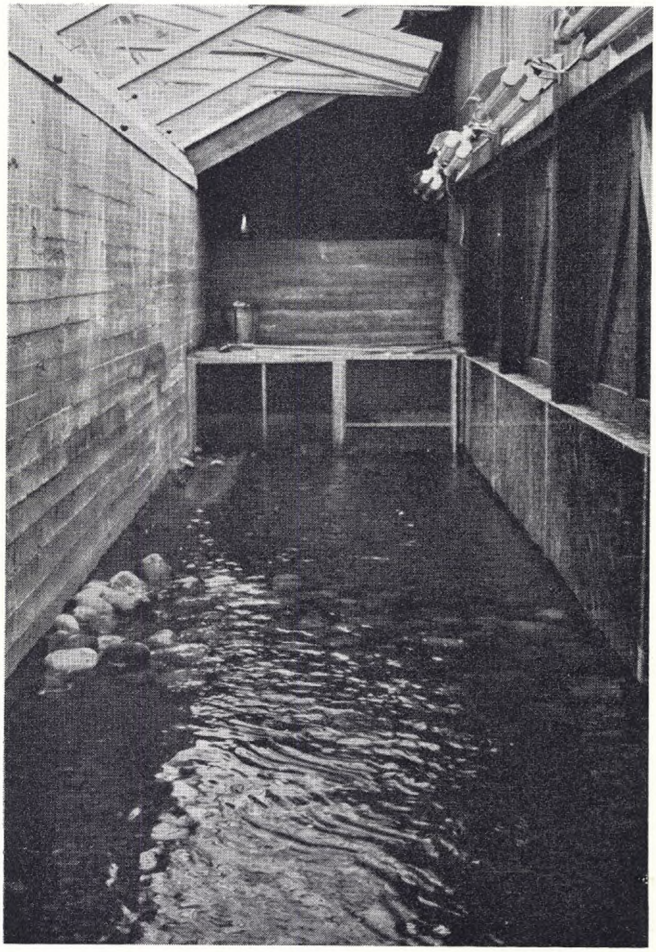

Fig. 3. Upstream view of the tank. (Photo: SVENONIUS.)

The aquarium has so far been used for studies of the biology of salmon and trout parr and of the spawning of whitefish (FABRICIUS and LINDROTH 1954). It provides great possibilities for further investigations on the biology of stream fishes.

Summary

At the salmon laboratory of the Migratory Fish Committee at Hölle on the River Indalsälven a stream tank 10×2 meters with an observation chamber along one of the long sides has been constructed for study of the biology of migratory fishes, especially in the young stages. The supply and level of the water can be varied within wide limits. Interesting observations have already been made, for instance, on the behaviour of young salmon under different environmental conditions, and on the spawning of river-spawning coastal whitefish.

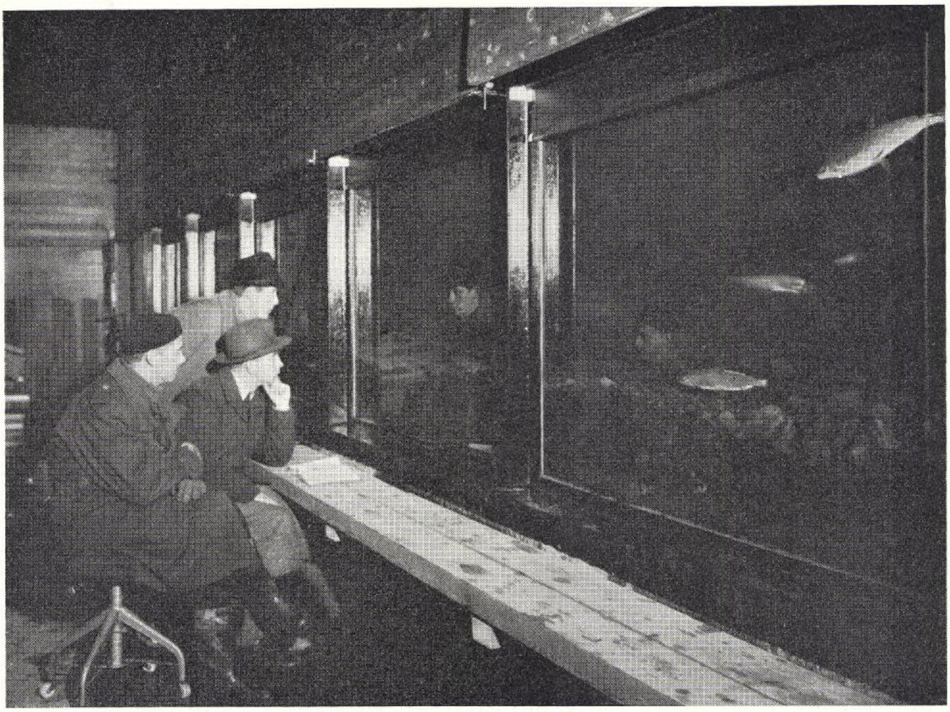

Fig. 4. Observations on the spawning of whitefish. (Photo: Fototjänst, Sundsvall.)

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Non-reproductive Migrations in the Char, *Salmo alpinus*, L.

By THOROLF LINDSTRÖM

Presentation of problem

The char is mainly a lake inhabitant in Sweden, gathering at certain shallow places during spawning time. Several cases are, however, known where the char moves up the tributaries for spawning and sometimes the char seems to be a more permanent inhabitant in running water, perhaps where the competition from trout is not so keen.

FABRICIUS (1950) has shown how the exclusive lake spawning has been affected in a lake, where heavy environmental changes were introduced through the regulation of the water level within a range of 11 metres. A considerable fraction of the char population began to spawn in the tributaries. FABRICIUS analyses the problem why the char spawn in the lake or in the running water.

In the present paper the movements of non-spawning char in a lake, where the char movements are of the normal Swedish type, will be illustrated by some experiments. A case will be reported where the regulation of the water level of two lakes is accompanied by char movements down in the outflow, involving immature and maturing char.

Presentation of localities

The material was obtained from Långan and Vålån, two tributaries of the River Indalsälven, Jämtland, and from the lakes where the River Ume älv originates in Lappland (Figs. 1, 2). The figures indicate the occurrence of char in the lakes. In both the Indalsälven and the Ume älv there is a deep lake on a lower altitude, where a minor char population exists (Storsjön, Storuman). In these lakes the cold hypolimnion may be a necessary condition for the existence of a char population. Whitefish, *Coregonus sp.,* dominates in these lakes and in some other lakes too on an intermediate altitude, which will be disregarded here (Lakes Ockesjön, Umnässjön and Gardsjön). Its natural distribution is barred upstream by falls and rapids. Sällsjön, Rönnö-

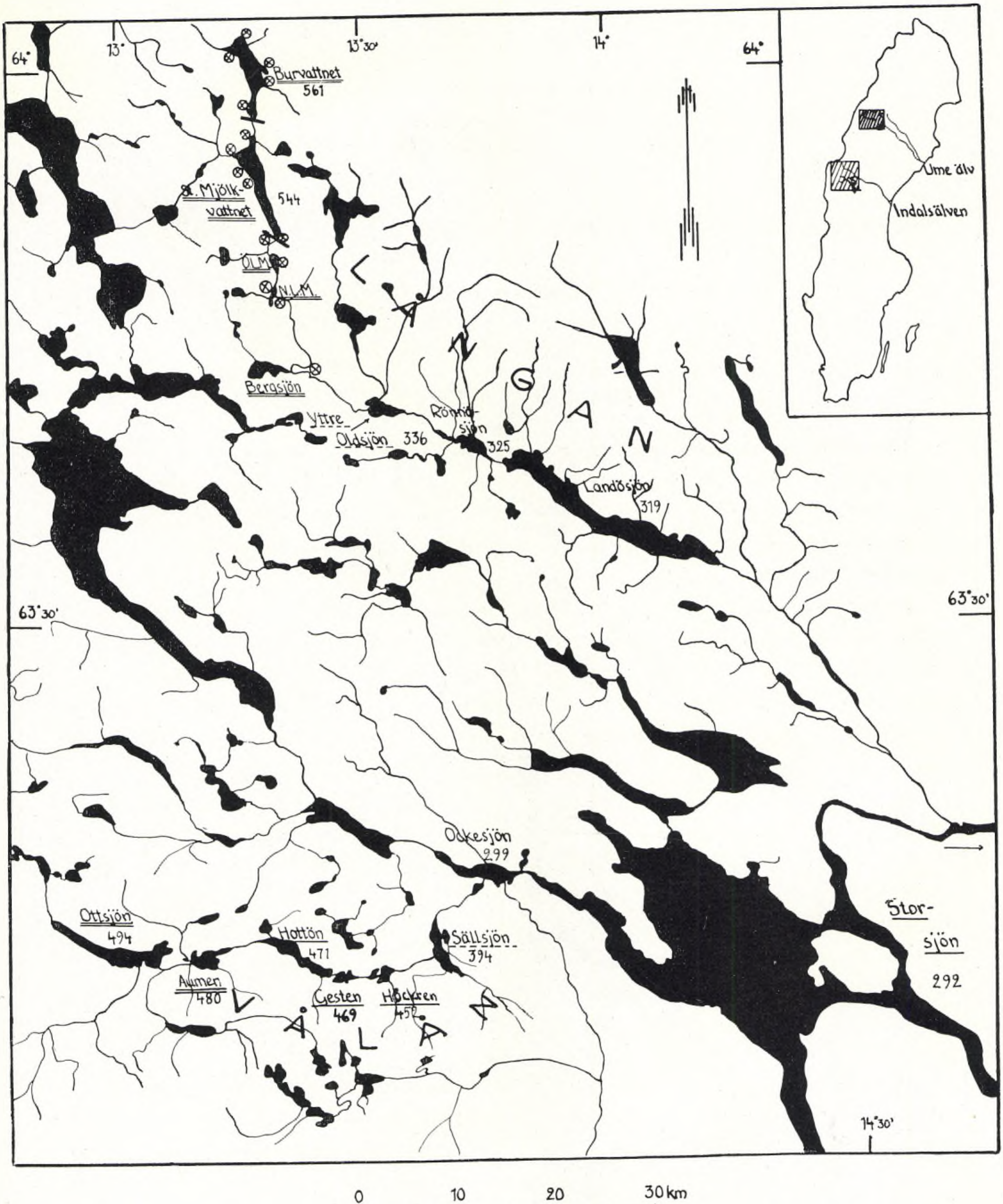

Fig. 1. The River Indalsälven district with Rivers Långan and Vålån. The general map of Sweden indicates the position of this district and the Ume älv district. The dams below Lakes Burvattnet and St. Mjölkvattnet are indicated with bars, perpendicular to the rivers. ⊗ = recaptures from the Långan experiment 1952. Altitude and char frequency is indicated for the nominated lakes: double underlining — char dominates or constitutes about 50 % of the fish population, single underlining — a medium or minor char population exists, broken line — only stray char are caught, no underlining — no char.

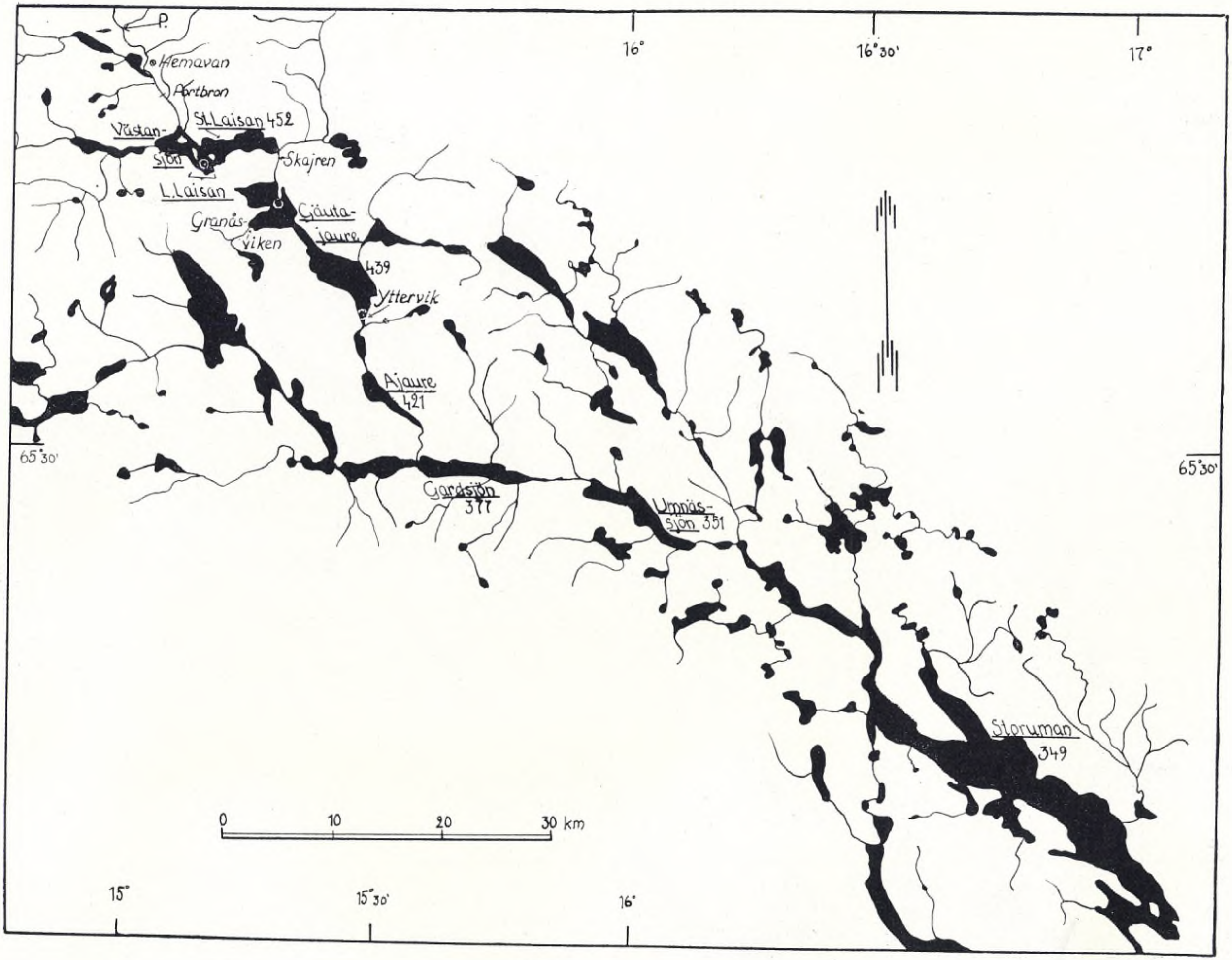

Fig. 2. The River Ume älv district. Altitude and char frequency as for fig. 1. ⊙=tagging places.

Table 1. Results from test fishing from Lake St. Mjölkvattnet (netting), illustrating the good fishing during the first decade following the regulation of the lake. Nets of various types, *i.e.* mesh size, were used. A variation in the composition of the set used the different years is disregarded here.

Year	Total number of fish per unit effort	Number of char per unit effort	Mean weight of char	Number of efforts (one net, one night)
1942	0.7	0.3	0.30	69
1943	1.4	0.5	0.32	48
1944	2.6	1.8	0.34	92
1945	2.2	1.6	0.32	142
1946	4.9	2.6	0.36	31
1947	2.9	2.1	0.24	75
1950	1.7	0.9	0.19	67

sjön, Yttre Oldsjön, Ajaur, Gäutajaure and Laisan were char-lakes of old. Whitefish was introduced into Lake Sällsjön, River Vålån, in the late 19th century. In the 1880's whitefish was already common and now char is very seldom observed and no char spawning is known. Whitefish was also introduced into a tributary of Lake Rönnösjön, River Långan, in 1915 and Rönnösjön and Yttre Oldsjön were transformed into whitefish-lakes in the 1930's. Char is now seldom caught in Lake Yttre Oldsjön and never in Lake Rönnösjön. No char spawning is known. (The last spawning char were big). In Lake Ajaur, River Ume älv, whitefish was introduced in the 1920's and is now common in Lakes Ajaur, Gäutajaure and Laisan, but considerable populations of char still exist in Gäutajaure and Laisan. The char seems to stand the competition from whitefish better than in the Indalsälven lakes, probably on account of the more northerly position and higher altitude of the Ume älv lakes.

Stray char caught in Lakes Sällsjön and Yttre Oldsjön nowadays are said to be »swept down» from the char lakes above. The author has only obtained one char from test fishing in Sällsjön and this one was caught immediately below the affluent from Lake Håckren. In the River Vålån many anglers are fishing in the running water between the char lakes, but char are not caught except stray specimens in the proximity of the lakes. Fishermen netting the running water between Lakes St. Mjölkvattnet and Yttre Oldsjön in the River Långan reported that they seldom got a char before the regulation of Lake St. Mjölkvattnet, in spite of the fact that the three small lakes in this section were dominated by char. The running water of the Rivers Vålån, Långan and Ume älv is inhabited by trout, and there are other species, both in the lakes and in the rivers, that will not be discussed in this paper. In 1942 big dams were built in the outflows from Lakes Burvattnet and St. Mjölkvattnet and the water levels have since been regulated within a range of 6 metres and

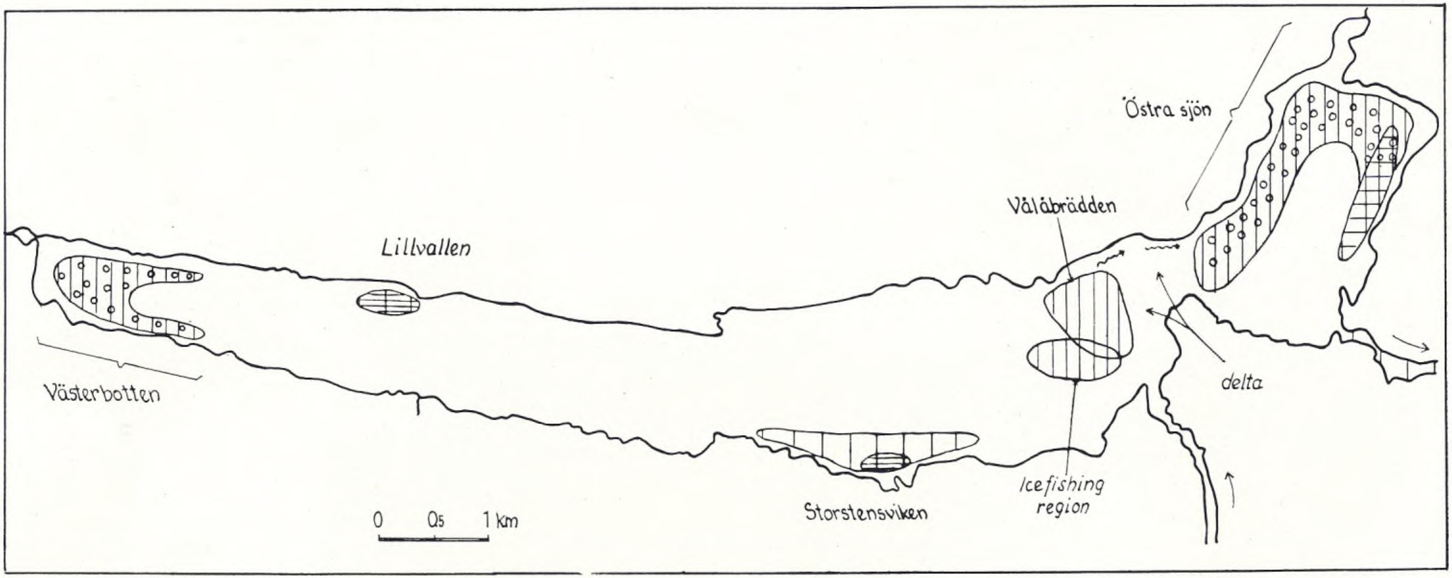

Fig. 3. Lake Ottsjön. °°° =tagging regions. ⊜ =spawning regions. ▥ =main fishing regions. Östra sjön, Vålåbrädden and Västerbotten are the most frequented summer fishing regions.

11 metres respectively. Most of the regulation range lies above the old water levels. A period of good fishing followed for these lakes, roughly illustrated in table 1. This regulation effect was analysed by RUNNSTRÖM (1951) for another lake. The fishermen reported smaller trout catches but a substantial increase in char catches for the running water below St. Mjölkvattnet.

The Vålån experiment

From the 15th to the 27th of July 1951 sixty-eight char were marked with numbered tags in Lake Ottsjön. Tagging places, main fishing regions and spawning places are indicated on fig. 3. Recaptures are tabulated in table 2. A bathymetrical map was published by LINDSTRÖM (1952). A comparison will show that the main fishing regions coincide with the more extensive shallow regions in the lake. The fishing region Vålåbrädden is situated at a sand delta, north of the main affluent. The delta is so shallow further east that much water is carried to Östra sjön through a groove following the northern shore. The current is perceptible in this groove. Västerbotten and Östra sjön are the only parts of the lake with considerable regions of submerged bottom vegetation (*Isoetes* etc.) The fishing is dominated by netting but otter fishing and other hook fishing are also important. The fishermen have made an estimate of their average yearly catches. The total was 3,500 kg, char constituting rather more than half the total.

Table 2. Recaptures from tagging in Lake Ottsjön 1951.

Time of recapture	Recaptures from 38 char tagged in »Östra sjön»		Recaptures from 30 char tagged in »Västerbotten»	
	Number	Locality (Fig. 3)	Number	Locality (Fig. 3.)
1951 July	5	Östra sjön	2	Västerbotten
August	2	» »	3	»
September ...	2	» »	—	
October	1	» »	2	Västerbotten and Lillvallen
1952 April	—		1	Icefishing region
May	1	Vålåbrädden	—	
June	2	Östra sjön	1	Storstensviken
July	2	» »	5	Västerbotten
September ...	—		1	Storstensviken
1953 June	1	Östra sjön	—	
1954 May	1	» »	—	
June	1	» »	—	

The Ume älv experiment

From July 25th to August 4th 1952 forty-three char were tagged in Lakes Gäutajaure and L. Laisan and in the river at Hemavan. An additional 76 were tagged 3/9—12/9 1952 and 31/8—10/9 1953 at Hemavan. Tagging places are

Table. 3. Recaptures from tagging in the Ume älv system 1952 (Fig. 2).

Time of recapture	Recaptures from 10 char tagged in Lake Gäutajaure (northern part)		Recaptures from 22 char tagged in Lake L. Laisan		Recaptures from 85 char tagged in the river at Hemavan	
	Number	Locality	Number	Locality	Number	Locality
1952 August . . .	—		4	2 in L. Laisan and 2 in L. or St. Laisan	—	
September	—		2	L. Laisan	1	Portbron
October . .	1	Granåsviken, Gäutajaure	—		—	
November	—		2	L. Laisan	—	
1953 June	—		1	L. Laisan	1	Hemavan
July	1	Skajren, St. Laisan	—		—	
October . .	—		1	L. Laisan	—	

No recaptures are reported from two char tagged at Yttervik, Gäutajaure.

indicated on fig. 2, recaptures are given in table 3. The tagging was originally carried out to verify a spawning migration from Lake Gäutajaure through Lake Laisan to point P. on the map, a migration which was reported by the fishermen. Fishing is carried on along the greater part of the presumed migration stretch, but more intensively in the lakes.

The Långan experiment

The outflows of Lakes Burvattnet and St. Mjölkvattnet are barred with dams, so that char in all probability cannot pass upwards except for a short period in late winter when the water levels of the lakes are as low as the water levels of the streams below — provided the char is capable of forcing a rapid in that cold water. During the experiment the water speed through the deep sluice gates was about 10 metres per second and the steep fall from the high-water sluice gates was about 6 metres in Burvattnet and 10 metres in St. Mjölkvattnet.

Fish traps were built in the summer of 1952 below the dams. For position and details see fig. 4. My thanks are due to Mr Lundblad and Mr Granström who managed the traps in 1952. The traps were constructed with vertical iron bars and iron net, diameter of slots and meshes not exceeding 2 cm. The Burvattnet trap worked August 1st—30th and September 10th—November 30th. The St. Mjölkvattnet trap worked from July 25th—December 3rd 1952, but only barred the branch from the deep sluice. In addition the water level somewhat exceeded the top of the St. Mjölkvattnet trap arms now and then between August 26th and September 12th. Concerning the efficiency of the

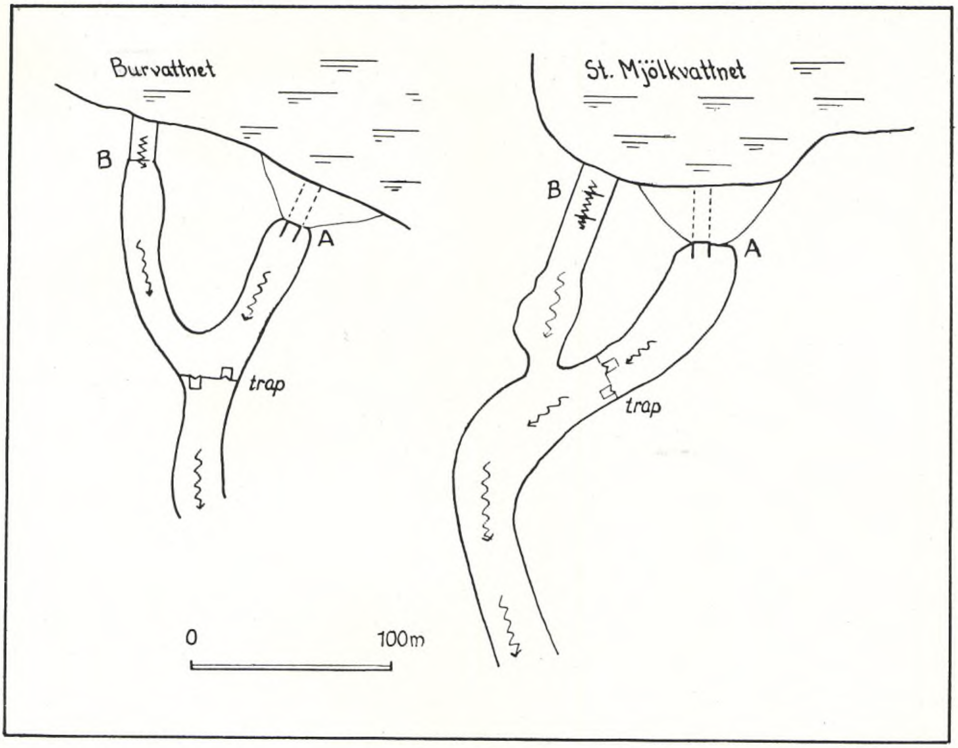

Fig. 4. Sketches of the dams and outflows from Lakes Burvattnet and St. Mjölkvattnet with highwater sluices (B) and deep sluices (A). Position of traps 1952.

traps, the author is not convinced that all fish were caught, which would have passed downwards if the traps had not existed.

Fish trapped while going downstream were helped over the trap to the downstream side and those trapped on their way upstream were carried to the lake. The left pelvic fin was cut.

In 1954 the trap below Lake St. Mjölkvattnet was rebuilt and worked from July 28th—30th.

The char were moving at night as most of the fish were caught in the morning controls. 404 downstream moving char were dead in September 1952 (Lake Burvattnet) and October—November 1952 (Lake St. Mjölkvattnet). Greater flow and lower temperature may have co-operated in achieving this result (Fig. 5). The water velocity for this period is estimated as not exceeding 2 metres per sec. at the St. Mjölkvattnet trap and 1 metre per sec. at the Burvattnet trap.

The weekly catches from the traps in 1952 including recaptures in the traps, are listed in table 4. Length distribution of these char is illustrated in fig. 6. Recaptures of char from the 1952 experiment are illustrated in fig. 1. The re-

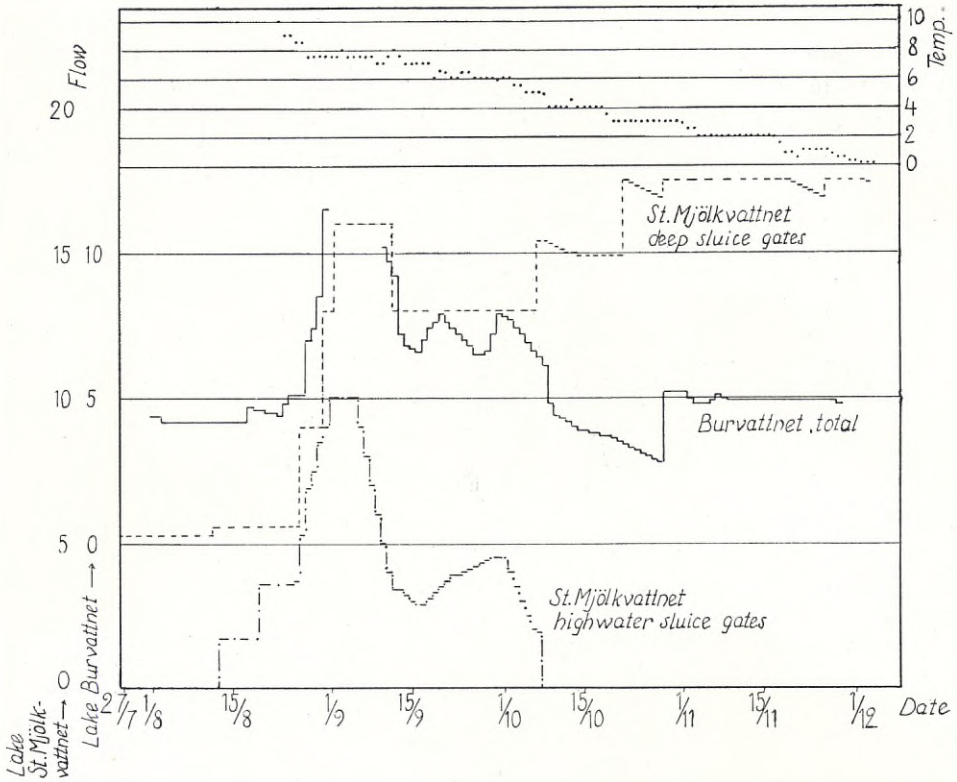

Fig. 5. Flow and temperature from the Långan experiment 1952. Flow in cubic metres per second, 8 a.m. (According to *Indalsälvens Regleringsförening.*) Temperature (only the stream below St. Mjölkvattnet) in ° C, 8 a.m.

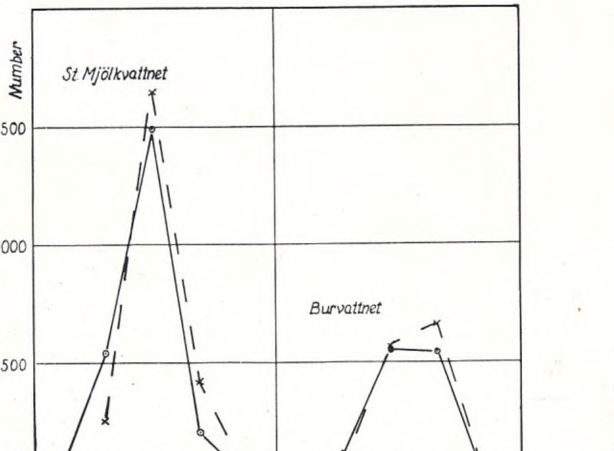

Fig. 6. Length distribution of char from the Långan experiment 1952. Broken line — upgoing char, unbroken line — downgoing char.

Table 4. Weekly catches of char from the Långan traps, 1952. Furthermore 95 trout and 12 burbot were caught in the Burvattnet trap and 19 trout and 3 burbot in the St. Mjölkvattnet trap. Five of the burbot were trapped on passing upwards. During the first two weeks (25/7—7/8) 206 downgoing and 594 upgoing char in the St. Mjölkvattnet trap were not fin cut.

Lake Burvattnet					Lake St. Mjölkvattnet				
Week	Downwards	Earlier fin cut	Upwards	Earlier fin cut	Week	Downwards	Earlier fin cut	Upwards	Earlier fin cut
					25/7—31/7	140	—	566	—
1/8—7/8	12	—	334	2	1/8—7/8	120	—	743	—
8/8—14/8	7	1	549	3	8/8—14/8	156	—	416	3
15/8—21/8	11	1	116	2	15/8—21/8	37	—	210	—
22/8—28/8	5	2	125	—	22/8—28/8	57	—	157	—
29/8—30/8	—	—	23	—	29/8—4/9	114	—	44	—
					5/9—11/9	82	—	18	—
10/9—16/9	107	—	92	—	12/9—18/9	118	3	39	2
17/9—23/9	112	—	44	—	19/9—25/9	120	—	41	—
24/9—30/9	212	—	30	—	26/9—2/10	166	2	48	5
1/10—7/10	88	—	21	—	2/10—9/10	183	6	37	—
8/10—14/10	81	—	6	—	10/10—16/10	166	12	9	2
15/10—21/10	47	—	2	—	17/10—23/10	128	11	11	1
22/10—28/10	59	2	2	—	24/10—30/10	102	3	2	1
29/10—4/11	55	—	—	—	31/10—6/11	27	1	2	1
5/11—11/11	180	—	—	—	7/11—13/11	53	3	—	—
12/11—18/11	167	1	—	—	14/11—20/11	184	8	—	—
19/11—25/11	66	—	—	—	21/11—27/11	192	2	—	—
26/11—30/11	22	—	—	—	28/11—3/12	104	—	—	—
Sum	1231	7	1344	7		2249	51	2343	15

ports of recaptures are not complete and the figure does not illustrate the frequency of recaptures from different localities. About 250 recaptures are reported (excluding the trap recaptures), mainly from the years 1953 and 1954. Most of the recaptures were made in the small lakes Ö.L.M. and N.L.M.

The 1954 catches from the St. Mjölkvattnet trap are listed in table 5, length distribution and development of gonads (from samples 1954) are tabulated in tables 6 and 7. Mean weight for a sample of 20 upgoing char: 152 g. Recapture was made of two char fin cut 1952. The temperature record in table 8 probably illustrates a temporary rise of hypolimnion water to the surface at the southern end of St. Mjölkvattnet — a strong southerly wind was blowing along the lake on the 28th. On the 30th the warm surface water layer was returning to the dam.

Table 5. Records from the 1954 trap at Lake St. Mjölkvattnet. Downgoing char not tabulated here as the arrangements were not quite satisfactory; only a few were caught.

Date	28/7	29/7		30/7			
Hour of control	7 p.m.	7—12 a.m.	7—8 p.m.	0—1 a.m.	2 a.m.	8—10 a.m.	5 p.m.
Catch, char going upwards	start	64	5	10	0	20	5

Table 6. Length distribution of a char sample from the 1954 trap catch (upgoing char).

Length, cm	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Number	1	2	0	0	1	5	4	0	8	6	11	14	14	11	3	2	2

Table 7. Gonad development of a char sample from the 1954 trap catch (upgoing char). Classification: Immature females — ovary 1/3 (group 1) or 1/2 (group 2) of the abdominal cavity. Eggs small, the diameter of the largest about 1—2 mm. Maturing females — ovary length 3/4 (group 3) or equalling (group 4) the abdominal cavity. Eggs maturing (enlarging). Immature males — testes are thin purple strings (group 1 and 2). Maturing males — testes yellowish-white, irregularly (group 3) or wholly (group 4) dilated.

	Females				Males		
Group	1	2	3	4	1+2	3	4
Frequency	8	13	10	11	15	1	3

Table 8. Temperature in the stream below the lake and in the surface of the lake near the dam, St. Mjölkvattnet 1954.

Date	28/7	29/7				30/7				31/7
Hour	7 p.m.	7 a.m.	12 a.m.	4 p.m.	8 p.m.	1 a.m.	9^{30} a.m.	1 p.m.	4 p.m.	4 a.m.
Temp. stream °C	9	6 1/2	6 1/2	6 1/2	6 1/2	6 1/2	6 1/2	7	8	8 1/2
Temp. lake °C		6 1/2						9		8 1/2

Discussion

Reports from the fishermen indicate that the char movements in the Vålån river system are of the normal Swedish type, and there is nothing in the author's material contradicting this. The interpretation of recaptures from tagging experiments is, of course, dependent on intensity and distribution of fishing. For the period roughly April-October the fishing in Lake Ottsjön is rather intensive. This is confirmed by the high recapture proportion (50 %). In April before the breaking up of the ice, icefishing (hook fishing) is concentrated to the region off the main affluent. From May to early September the fishermen visit all parts of the lake but most of the fishing is concentrated to three main summer fishing regions: Östra sjön, Vålåbrädden and Västerbotten (Fig. 3). To a great extent the fishing regions Östra sjön and Västerbotten cover the regions where the tagging was done. For the period late July —early September 1951 the results from the experiment should be conclusive. The conclusion one may draw is that an exchange of char does not ordinarily occur between Östra sjön and Västerbotten, nor does char from these regions ordinarily visit Vålåbrädden. Perhaps the shallow sand delta and the groove with its weak current act as a hindrance, fencing off char which otherwise would pass between Östra sjön and the other parts of the lake. There is, however, an explanation, which is more likely: Östra sjön and Västerbotten are shallow regions where char is feeding. Adult mayflies and caddis-flies, for instance, emerge here abundantly in July and one reason for the concentration of tagging and fishing to Östra sjön and Västerbotten is the fact that char is easy to catch here during July, using an otter (artificial flies). Occasional swarms of plankton exist in the shore regions (LINDSTRÖM 1952) but otherwise the scanty plankton samples from Östra sjön and Västerbotten do not indicate high plankton abundance.

During late September and early October the mature char concentrate on the spawning places indicated on fig. 3, and the fishing is confined to these regions as well. Few tagged char are recaptured during spawning fishing and spawning migration will not be discussed. During the rest of the autumn and the winter, fishing intensity is low. Those few recaptures indicating long distance movements are made in the autumn or spring and early summer. The recaptures may indicate spawning migrations or a combination of spawning migrations and other (winter) migrations. One may conclude that the char do return to the summer dwellings they occupied last summer if they move about for the rest of the year.

Turning now to the running water it can be stated that no tagged char are recaptured and only stray char are caught in spite of fairly intensive hook fishing during the summer months. Of course, one cannot wholly discard the idea that char does move in the running water in the River Vålån, but all the indications suggest that such char movements cannot be very important.

The reported spawning migration in the Ume älv district is here disregarded. The recaptures from char tagged in Lake L. Laisan suggest that char is stationary, but the suggestion may be false. Char does exist in the running water and pools at Hemavan where tagging is carried out but the low frequency of recaptures from this latter tagging shows that the fishing intensity is low in the Hemavan district. Should tagged Laisan char move up the river to Hemavan at any season of the year, there seems to be only a small chance of recapture there. One may, however, conclude that if the bulk of the Laisan char move away, they must return. One may also state that little is known at present of the movements of char in the Ume älv district but it seems important to give at least some particulars from a case where char is a more permanent inhabitant in unaffected running water.

Reports from the fishermen in the Långan system indicate that the char movements, before the dams were built, were of the same type as in the Vålån system. The trap experiment was carried out ten years after the dams were built and confirmed the reported accumulation of char in the running water after the regulation of the lakes. An accumulation of char below a regulated lake was reported by DAHL (1933) from Lake Aursunden in Norway and further indications of such accumulations were obtained at Lake Pålsbufjord in Norway (P. AASS, unpublished MS) and at Lakes Torrön, Stor Sjouten and Borgasjön in Sweden (verbal communication from S. RUNNSTRÖM and E. FABRICIUS). The accumulation of char below the Långan dams is a spectacular phenomenon. About 7,000 char were trapped in half a year. As the area of the lakes is about 2,000 hectares, a yearly catch of 10,000 kg. = 7,000 kg. char (cf. Table 1) = 50,000 char would be a very good total from these deep lakes. The fishing is in reality much less.

The low frequency of recaptures of fin cut char in the traps together with the different seasonal rythm in the upward and downward movements (Table 4) and the distribution of recaptures (Fig. 1) indicate two distinct long distance movements: upwards and downwards. Before proceeding it must, however, be stressed that the distribution of fishing and the frequency of recaptures from different parts of the Långan system is not very well known. It must also be stated that the recaptures were made mainly during the years 1953 and 1954. A spawning migration, for instance, during any of the years 1952—1954 may explain the distance between tagging place and recapture places. The Långan experiment, however, gives some illustrations of the movements of char in regulated lakes.

The downward movement of char lasted as long as the experiment (end of July—beginning of December). Many char were recaptured in the small lakes (Ö.L.M and N.L.M., fig. 1). The presumed supply of char to Lake Yttre Oldsjön is not verified but still quite possible. There seem to be some trends in the record of daily catches (not published) which may have resulted from the distribution and movements of char in the Lakes Burvattnet and St. Mjölkvattnet (shoaling) or from variations in the flow from the lakes. The material does not call for a study of correlation between flow and number of char passing downwards, but the material is not conclusive as the traps were situated 100 metres below the dams: the char could stop between the dams and the traps. The downward movement through the sluice-gates is not necessarily a passive sweeping down of the char. Perhaps the greater density of char in the shallow parts of regulated lakes does induce an active movement down into the outflow. A passive movement seems, however, most likely at present. The water velocity in the deep sluices of the Långan dams was about 10 metres/sec. and the transition from the lake to the running water is more abrupt than in an unaffected lake.

In some cases it is shown that the downgoing char did come from the lakes, in most cases one must also consider the possibility that they had moved up the river towards the dams earlier in the year and now returned, and then the interpretation of night activity and the relation between flow and downward movement gets difficult.

It is of considerable interest to note that the greater part of the upward movement, *i.e.* the only movement which must be active, takes place from the beginning of the experiment in late July (when it is already fully developed) to the end of August. The Vålån experiment and the Långan experiment are of an entirely different nature, as the latter is confined to a fraction of the char population, which is already moving in running water. The temperature in Lake Ottsjön is also generally higher than the temperature in the Långan lakes (cf Table 8 in the present paper and the diagrams in LINDSTRÖM, 1952) but still it is of some interest that char seems stationary in Lake Ottsjön during the period late July—early September. Even if we make allowance for the far-fetched hypothesis that a spawning migration could start in July in Långan and decline in late August, one month before the actual spawning, the upward movement in July—August is not exclusively a spawning migration as so many char of sex group 1—2 do take part (> 50 %). It may be better to interpret the upward movement as a search to regain the lake the char has been forced to quit. A long series of experiment should precede a statement about causality.

The big morning catches in the traps indicate greater night activity of upgoing char. A decline of temperature from 9° C to 6.5° C did not stop the activity in July 1954, but only few char moved upwards in the autumn 1952 when the temperature declined from 7—8° C. to 0° C

The char is by no means a typical lake inhabitant in all countries where it exists. GRAINGER (1953) has reported a case from Baffin Island where the whole char population, except the youngest year classes, moves down a river into the sea in the spring and returns up the river in July—September, presumably to a lake. Both maturing and immature char takes part in the upward migration. This upward movement recalls in some respects the upward movement in Långan. Should the similarity turn out to concern essential qualities, the heavy environmental changes following the regulation of lake levels have produced an interesting intermediate stage. There are, however, many differences too. Those char, for instance, moving downwards more than ten kilometres from Lake St. Mjölkvattnet have no opportunity of regaining the upper district again. It will be interesting to see if the presumed supply of char to Lake Yttre Oldsjön — once a char lake — will restore a char population in this lake. The whitefish must here compete with char recruits, which are already adult.

Summary

Some experiments give a fragmentary illustration of the non-reproductive movements of char. A case is reported, where char is seldom observed in running water. A tagging experiment in a lake belonging to this system indicated that char was stationary in a certain sense during the summer. Another experiment confirmed a reported accumulation of char in running water be-

low two lakes, where the water level was regulated. The accumulation is an effect of the regulation of the lakes. It seems most likely that the char is passively swept down from the regulated lakes. An upward movement towards the dams was also demonstrated, occurring in late July—August and involving both immature and maturing char. Causality is only discussed preliminarily.

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Investigations on the Organic Drift in North Swedish Streams

By KARL MÜLLER

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Introduction

T. BORGH (1927) and P. WOLF (1947) have drawn attention to the phenomenon that in running water there is a continuous stream of benthic organisms. Below the outlets of lakes these normally consist of plankters. KRIEGSMANN (1952) and, more recently, GEISLER (1953) have published reports from central Europe which show that the drift from lakes is made up of extraordinarily large quantities of material; this depends, of course, on the degree of eutrophication of the lake in question. In each of the streams investigated by us in the North Swedish forest zone we were able to observe, independently of the influence of a lake, a drift in which nearly all groups of benthic fauna were represented. Owing to the great importance of this phenomenon from the point of view of production biology, we carried out, in the summer of 1953, an exhaustive investigation to determine the nature and extent of the drift.

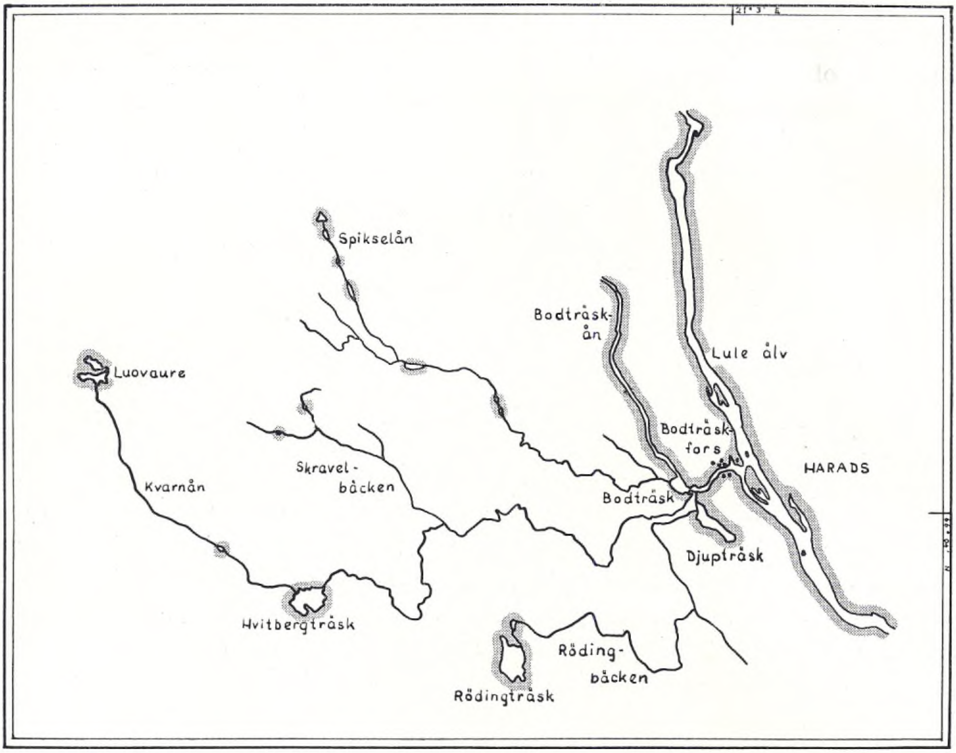

Fig. 1. Map of the area under investigation.

I. The Area under Investigation

The sketch in Figure 1 gives a general view of the site of the investigations in the Bodträsk river system. The Bodträskån flows into the lower part of the River Lule, not far from Bodträskfors. Our main observations on the amount and composition of the drift were made in a small forest stream, the Skravelbäcken. Additional investigations were carried out in the streams Kvarnån and Spikselån and in the lower reaches of the River Bodträskån.

II. Methodology of Investigation

In order to investigate the drift, nets were stretched across the stream under the water in such a way that they neither extended above the surface nor touched the bottom. The nets we used had a frame of steel wire (0.8 mm.). The wire projected on one side for about 1 m., thus serving to fix the net in the sloping bank. A prong projecting downwards served to anchor the net perpendicularly. In this way we made certain that the net remained in position, even when the pressure of water was fairly strong. Nets with plankton gauze or with 1 mm. mesh were used. The 1 mm. mesh could be used for observations lasting more than a day; plankton gauze clogs very quickly and usually cannot be left in the water for longer than 30 minutes.

The observation sites were chosen so that the net covered the middle of the stream.

The 1 mm. nets were generally left in the water for 12—24 hours. In order that the results could be expressed in standard units all values were calculated on the basis of a 24-hour observation period and a 1000 cm^2. area of net surface. Nets with surface areas of 200 cm^2, 1000 cm^2 and 2500 cm^2 were used.

III. Specific Investigations

The observations on the drift were made during the period 20th May to 30th October 1953. Our survey thus covered the period from the breaking up of the ice to the first freeze-up. Only at the beginning of leaf-fall, at the end of August, was it necessary to suspend our observations for a few weeks as the nets were too quickly clogged by the leaves that were carried along in the water and inaccurate values were to be expected on account of the backwash.

1.) *The quantitative extent of the drift.*

The investigations on the drift were carried out as part of an investigation on the productivity of North Swedish streams (MÜLLER 1953). When we were investigating the animal population of a newly regulated (cleaned-out) forest stream we found that re-colonization of the area took place in a remarkably short time (cf. also *op.cit.* p. 103). This rapid re-colonization was at first incomprehensible; it can now be largely explained in the light of our observations on the drift. Since it was necessary to make a survey of the drift quantitatively and qualitatively our investigations were concentrated mainly on the small forest stream Skravelbäcken. In 1952 we studied the bottom fauna in the upper reaches of the stream; these investigations were continued during 1953. In this way we obtained a general picture of all the important elements of the fauna. Moreover, as this stream lies well away from human habitation, the effects of civilization are eliminated and we consequently see a North Swedish stream in its natural state.

The graphs which follow show the amount of drift observed during the summer of 1953. Number (- - - -) and weights (——) are represented separately.

It will be seen that the numbers and weights of the individual components of the drift are at their peak in May. The values reached at the end of May are more or less maintained during June and July; in the middle of August a marked decrease can be observed. It is possible, however, that the values

Table 1. Survey of the potential total drift in the Skravel stream during the summer of 1953.

Date	Observed Drift 1000 cm²/24 hrs		Cross section of stream (m²)	Potential total drift in 24 hrs	
	No. of individuals	Weight (g)		No. of individuals	Weight (g)
24.5	288	2.80	2.8	6624	64.4
26.5	408	1.60	2.3	9384	36.8
25.6	252	0.348	1.8	4536	6.3
20.7	379	0.432	1.9	7101	8.2
7.8	275	0.385	1.9	5225	7.3
18.10	35	0.155	2.2	770	3.4

from about 17th August 1953 onwards were influenced by the incipient leaf-fall, since the nets used in the investigations were very easily clogged and, owing to the blockage and the backwash, not all the organisms present were caught in the net. The october values were about the same as those observed at the end of August.

Various explanations can be given to account for the exceptionally high May values. The mechanical influences on the floor of the stream are, no doubt, greatest at this time. The breaking up of the ice and the high water are external factors which promote or facilitate the transport of benthic organisms downstream. The great weights obtained can be explained by the fact that large numbers of aquatic larvae are at this time almost ready for flight or pupation and have thus reached their maximum size as larvae. This fact is reflected particularly in the ratio between numbers and weight; similar ratios are not reached again until the month of October.

Since we have expressed the results in terms of a standard unit (1000 cm² of catching surface/24 hours) it is interesting to calculate the value of the total drift. Obviously the drift is not equally great in all parts of the cross-section of a stream; those parts nearest the bank, for example, can be disregarded altogether. The total drift should only refer to an area where the type of current is more or less the same; that is to say, we chose only the more central region of the stream in which, ideally, a laminar current is present. In the experiments described here the measurements and calculations during the summer half-year were always made at the same place, about 200 m above the point at which the Skravelbäcken flows into the river Kvarnån. The average speed of the current upstream of the net was 0.50—0.70 m/second.

Even if these values for potential total drift are not completely accurate due to the fact that the region of the current cannot be exactly defined, nevertheless, in practice, the figures for total drift will be of the same order

Table 2. Determination of the drift with a plankton net.

Date	Observed Drift 1000 cm²/24 hrs No. of individuals	Weight (g)	Cross section of stream (m²)	Potential total drift in 24 hrs No. of individuals	Weight (g)
27.5	15110	4.79	2.3	332420	110.17

of magnitude. Probably they are substantially higher, a view which is confirmed by the next experiment.

In the experiments so far described we worked with nets with a 1 mm mesh. On 27th May 1953 we used a specially constructed plankton net. This 'drift net' consisted of a square brass frame, 50×50 cm, carrying a 1 m long linen bag, the floor of which was made from 50×50 cm of Müller's gauze. The net was weighted with stones and placed in the current.

If the same calculations are made for this experiment as for the one described above very different numerical values are obtained.

Chironomidae (*Orthocladiinae, Podonomidae, Cardiocladius* and various lake forms) and *Simuliidae* were the main components of the drift, but *Trichoptera* (*Plectrocnemia*), *Hydracarina, Plecoptera* and *Ephemeroptera* were also found.

The above experiment demonstrates that only a portion of the actual drift is caught with 1 mm nets. Owing to lack of time it was not possible to make regular investigations with the plankton net in the summer of 1953; this work will be held over for special investigations in the summer of 1954.

Comparative investigations were made with the 1 mm nets in different parts of the area. The results varied greatly according to the time and position of the investigation site.

Since the data in Table 3 represent the results of investigations made at different sites the figures require some elucidation.

The observations in the River Kvarnån on 2nd June, 1953, were undertaken when the river was in spate. About 2 km upstream from the observation

Table 3. Observations on the drift in various sections of the river system.

Date	Place	Observed Drift 1000 cm²/24 hrs No. of individuals	Weight (g)	Cross section (m²)	Potential total drift in 24 hrs No. of individuals	Weight (g)
2.6	Kvarnån	3840	5.76	5.0	192000	288.0
11.6	Kvarnån	445	0.425	6.0	26700	25.5
1.6	Bodträskån . .	920	1.20	8.0	73600	72.0
27.5	Spikselån . . .	120	0.89	4.2	5040	37.4

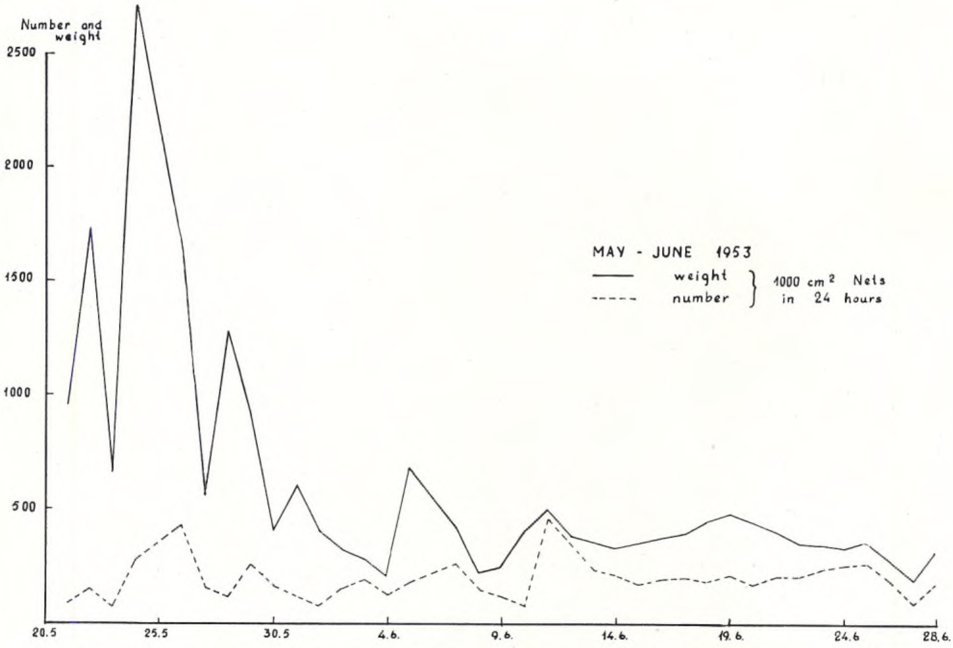

Fig. 2. Number and weight of drift in the Skravelbäcken, May and June 1953.

site there is a reservoir (Kvarnådamm) which is periodically impounded. When the dam is opened a wave of high water sweeps down the lower course of the river. Our observations were made at the time the water was released. The exceptionally high values can be explained by the mechanical effect of the flood water. Nine days later the drift was very much reduced in amount. Its qualitative components were also basically different (see also Fig. 4.)

The observation site in the Bodträsk River lies downstream from the Bodträsk Lake. Due to the drift from the lake, elements of the lake fauna are well represented. In the Spikselån the quantitative relations are about the same as those found in the Skravelbäcken.

In summing up, we may state that, as can be seen from Figures 2 and 3 and Tables 1—3, the drift plays an important part in the production cycle of running water. It is therefore not enough to regard the amount of bottom fauna in a strictly localised site only as 'capacité biogénique' in HUET's sense. A proper conception of the benthic elements from the point of view of biological productivity must also take the drift component into consideration.

2.) *The qualitative composition of the drift.*

Decisive for an evaluation of the drift is a quantitative and qualitative comparison with the bottom fauna in that part of the stream lying above

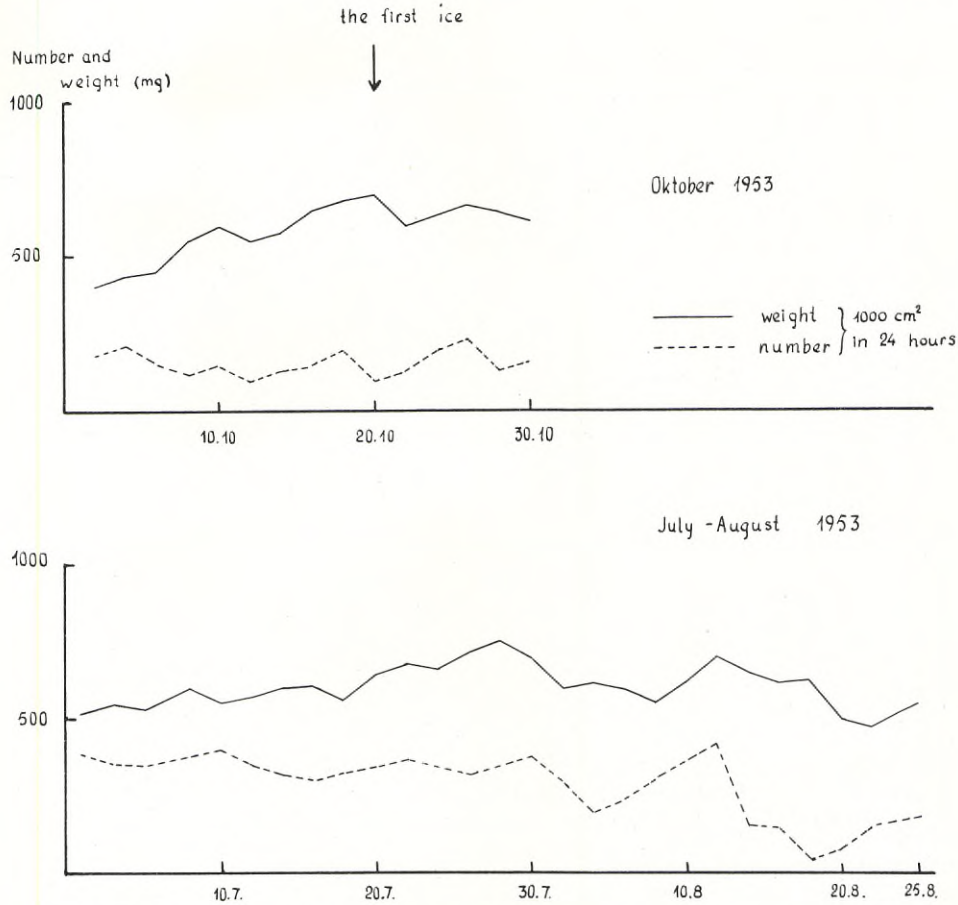

Fig. 3. Number and weight of drift in the Skravelbäcken, August and October 1953.

the observation site. The comparison shown in Figure 5 was made in such a way that average population at the given periods was noted for all the investigated portions of the stream Skravelbäcken lying above the site of the drift observations.

Further downstream the qualitative components of the drift at the same periods of time were noted. In this way the proportions of the individual components of the benthos present in the drift can be clearly seen.

The first thing that strikes an observer is that particular groups of animals (*Hydracarina* and *Coleoptera*) often form a relatively large portion of the benthos population but very seldom occur in the drift. This is probably due mainly to the mode of life of these animals, which are usually found only among thick plant growth on stones and so largely avoid all mechanical influences. As for the other groups of animals, the June figures show clearly that these occur in roughly the same proportion as in the benthos. Only in

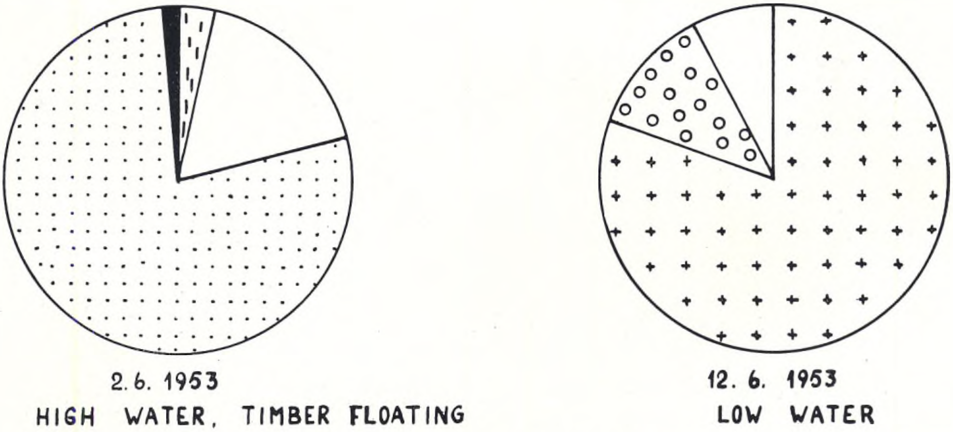

Fig. 4. Changing quality of the organic drift in River Kvarnån in ten days. For explanation of the symbols see Fig. 7.

the case of the *Chironomidae* was the proportion significantly higher in the drift. It was observed, however, that very many lake forms of *Chironomidae* had been washed in; hence it is easy to understand why the picture is somewhat distorted. The same is true for the month of July, when the main flight period for species in running waters is past and a reduction can be seen in the numbers of Chironomid larvae. In the case of the *Ephemeroptera,* whose imaginal phase is already over at the beginning of June, the young larvae (*Chitonophora*) appear in the drift in large numbers as early as July. In the *Trichoptera* pupation is beginning, so it is understandable that this group of animals decreases considerably in the drift. We have already indicated above the differences in the representation of the *Coleoptera* and *Hydracarina.*

For the month of August there was almost complete agreement between the percentage distribution of the bottom fauna and that of the drift. Only the *Chironomidae* were less well represented in the bottom fauna, as in the previous months.

Attention has already been drawn to the fact that determination of the drift with 1 mm nets does not give results which are completely accurate quantitatively. The experiment with the plankton net showed that the yield is very much higher with a fine-meshed net.

In one experiment it was in fact possible to obtain an almost exact picture of the real extent of the drift.

On 4th June 1952 about 150 m of the lower course of the Skravelbäcken was cleared with the help of caterpillar tractors. At the same time a completely new bed was made for the stream. The main characters resulting

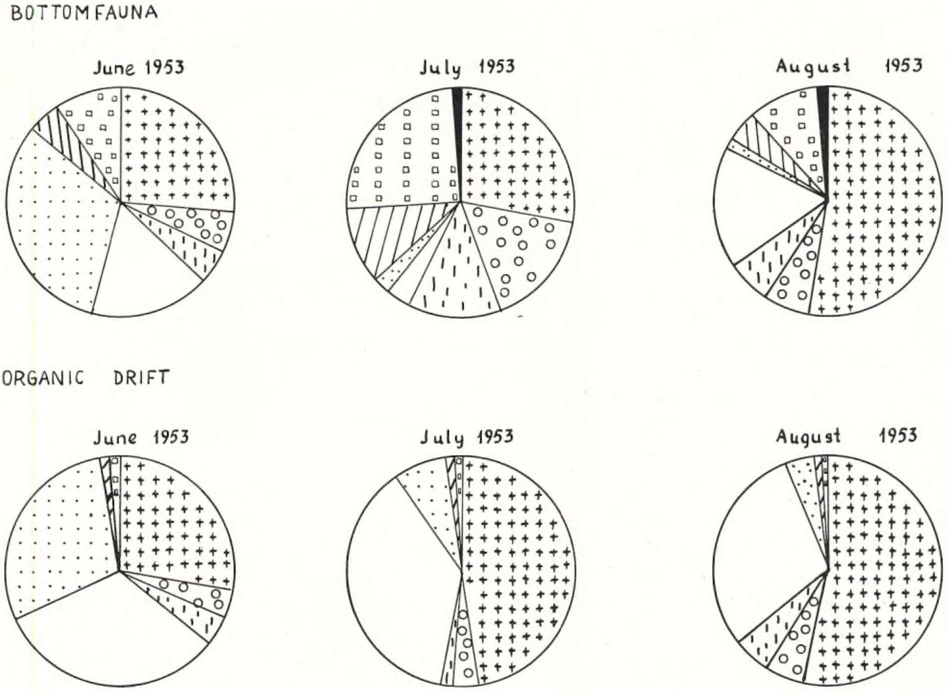

Fig. 5. Comparison between the quality of bottom fauna in the upper course of the Skravelbäcken and in the drift in the lower reaches of the same stream. For explanation of the symbols see Fig. 7.

from the change were an increased rate of stream flow and an altered stone structure (all fairly large stones being removed). We may assume that no animal population existed immediately after this operation.

Eleven days later a thorough investigation was made of the new bed of the stream. The results of 10 separate samples indicated on the average a population of 924 individuals per 1000 cm^2 and a corresponding weight of 1010 mg/1000 cm^2. The average breadth of this section of the stream was 3 m, corresponding to a surface area of 450 m^2. Thus, during the said period of 11 days, 4,158,000 organisms weighing 4.55 kg had made their appearance.

If we generalise the finding of 27th May 1953 (evaluation of the drift with a plankton net) so as to cover an 11-day period we get a drift of 3,656,620 individuals, which is very close to the value observed above, at least as regards order of magnitude.

The various examples that could be taken of the quantitative and qualitative range of the drift show clearly that in running water a travelling benthos is present as well as, and to the same extent as, the strictly localised benthos. Our observations showed that this travelling benthos (drift) was found during the whole period of the observations and that we must regard it as a constant factor of running water fauna. In the following section we shall analyse the causes of this phenomenon.

IV. The Causes of the Drift — the Colonization Cycle

No exact evidence is available regarding the cause of the drift. It is, however, worth while making the following comments. The distinctive characters of a lake — an enclosed living space — are absent in running water. The latter is entirely different from the former in physiographic factors, such as chemical processes, temperature, constant movement, and in its flora and fauna.

Although many water organisms have the capacity for active migration, it is nevertheless true that in the case of many organisms in flowing water or water with a strong current, movement upstream is limited or impossible. This is particularly true of mass forms. A *Simulium* larva, for example, lacks any organs of locomotion which would enable it to overcome the rapid flow of a stream. The Trichopteran larvae which were frequently found in the area of our investigations (*Neureclipsis bimaculata, Plectrocnemia conspersa* and even *Hydropsyche sp.*) could hardly travel upstream for any great distance. Migration, or an extension of the range of the larvae, can therefore only take place downstream, the organisms using the current as a mean of transport. The present investigations show that a continuous drift exists during the whole summer; it fluctuates in its values but never quite ceases.

If we carry these arguments to their logical conclusion it follows that the upper portion of the stream must steadily become depleted. However, as investigations on the amount and composition of the bottom fauna show, such a depletion of the upper reaches of a stream does not in fact occur.

There must therefore be a natural regulating factor, in as much as many forms deposit their eggs in the upper reaches of the stream. At these points there is at first a great abundance of eggs and larvae. Some observations made by various zoologists may be quoted here. Thus SCHÖNEMUND (1930) observed a swarm of *Caenis macrura.* »The whole swarm flew upstream at walking pace. New animals continually emerged from the water and joined in, so that the cloud became larger and larger. I was able to follow the swarm for a distance of 1 km until it flew onwards over an inaccessible meadow.« Continuing SCHÖNEMUND draws the conclusion: »No doubt this flight serves to ensure the continuance of the species, since the larvae, during their long period of development in mountain torrents, are often carried far downstream, and thus the eggs must be deposited fairly high up the stream.« ULMER (1927) quotes a report by STADLER on *Polymitarcys virgo* in which he says that he was able to observe these *Ephemeroptera* flying for a distance of 2 km as the crow flies at a height of 200 m. In our investigations this phenomenon was quite striking in the case of the *Simuliidae*. Even in parts of the lower course of the stream where Simuliid larvae were plentiful the imagines were found relatively seldom. A distinct accumulation occurred, however, below lake outlets and in the lake of origin.

If we accept the fact that, for some of the principal animal forms of the benthos, an accumulation of eggs occurs in the upper reaches, then it follows that a rapid reduction must take place in the available living space, especially during the weeks of quick growth in early summer. The basic food of the various larval forms is limited, and an increase in requirements (resulting from the rapid increase in growth) must inevitably lead to keen competition if the number of organisms remains the same. Moreover, especially in the early summer months following the spate at the beginning of summer, a marked fall in the water level occurs, accompanied by changes in the speed of the current and a reduction in the available living space. Thus, even on the basis of these arguments, a series of factors can be found which determine the 'induction of the drift'.

In order to clarify the problem of the cause of the drift we must start by considering the basic differences between standing water (lakes) and running water. THIENEMANN (1953) has dealt with the question of rivers and lakes in a short treatise and has pointed out the fundamental differences between the two types of water from the limnological point of view. Important for the problem we are dealing with here is the fact that a lake represents a closed system which is autarchous and forms an isolated unit. A river, on the other hand, lacks this typical characteristic of standing water. In particular we must remember here the seasonal changes in the water level of both types. A lake may, indeed, overflow its banks. Such fluctuations can, however, be regarded as unimportant compared with those of a river. Even a heavy thunder shower in the height of summer can entirely change the basic current relationships within a few hours. These very different conditions postulate quite a different fauna, adapted specifically to the living conditions which prevail in running water. On the other hand, they make it appear likely that the percentage of animals lost will be higher than in the closed system of a lake.

So it seems understandable that nature is making use of a mechanism, and that, as here postulated, there occurs a migration of imagines upstream, which, following the direction of the stream, ensures a balance and a completion of the population. The drift is a link in the chain that, starting out from an over-abundance of progeny in the upper reaches, regulates and maintains the population with the help of the current. For if the various individuals that make up the fauna of running water could not make use of the drift, they would be annihilated owing to the increased competition resulting from variations in the size of the living space and the increasing food requirements in summer.

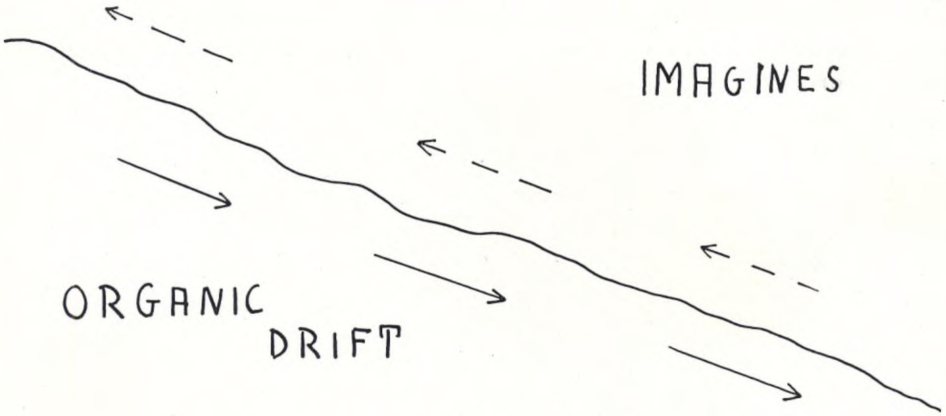

Fig. 6. Diagram of the colonization cycle.

The phenomenon of drift is, moreover, not confined to the types of animal whose imagines, in the form of flying insects, are capable of travelling long distances outside the water. It is known that *Salmo trutta* also travels back upstream for long distances for spawning. Besides providing favourable conditions of growth for the young fishes in the higher reaches of the stream, this enables the fish larvae, which are capable of active movement only to a very limited extent, to be distributed over a fairly wide area without the expenditure of much energy.

It is justifiable from these observations to assume a regular cycle for the groups of animals mentioned. The adult forms migrate against the current, while oviposition always occurs at the upper limit of the natural habitat. The organisms are distributed with the help of the current. For this phenomenon the term 'colonization cycle' (Besiedlungskreislauf) is proposed. (Cf. also Fig. 6.)

The question of the colonization cycle of various other groups of animals inhabiting the stream biotype (*Hydracarina, Coleoptera, Mollusca, Crustacea*) remains, for the time being, unanswered. In the case of the first-mentioned (*Hydracarina, Coleoptera, Mollusca*) natural adaptations are present which prevent the occurrence of these animals in the drift. These forms possess strong organs of attachment which enable them to overcome even fairly swift currents and at the same time limit mechanical drift; or they settle on the undersides of stones or in thick cushions of moss on the stones which are not directly affected by the current. The reduction in the size of the living space due to too great an animal population in a restricted habitat may be counteracted here also by migration. In the case of the Crustacea, especially *Gammarus,* no explanation of the problem is available. In the investigations of WOLF (1947) *Gammarus* was observed in the drift in very large numbers.

Huet (1941), on the other hand, indicated that the absence of *Gammarus* from some Belgian streams was due to the too strong »flushing capacity of the current».

V. The Importance of the Drift from the Point of View of Biological Productivity

Owing to the extent of the drift in running water, it is clear that this phenomenon is of importance in the production cycle. Its importance lies in the fact that eggs laid in particular concentrated areas are distributed during the development of the animals in such a way as to allow optimal utilization of the food supply available for the different organisms. On the other hand it must be presumed that the drift is also used by fish as a source of food.

The experiment illustrated in Figure 7 was carried out at a site in the lower course of the River Kvarnån. First of all a determination was made of the drift at this point during the period from 2nd to 6th June 1953. On 6th June a population survey of the bottom fauna took place. On 5th June the stomach contents of 5 *Thymallus vulgaris* and 5 *Salmo trutta* were investigated. It was found that the food picture of the trout was largely in agreement with the distribution picture of the fauna of the drift at the point in question. There were in addition some fishes (*Phoxinus laevis* and *Salmo trutta*) and, to a lesser extent, *Mollusca, Trichoptera* and *Plecoptera.* Such a food picture is understandable if a trout is observed feeding in a stream. It is found that the fish usually takes up its position at a place where there is little current and shoots forward to catch its food in open water. The proportion of fishes among the stomach contents also supports this view.

The grayling behaves in quite a different manner. It usually stations itself in the midst of the current, in or under submerged plants or behind medium-sized stones, and takes its food directly from stones or from plants on the floor of the stream. This behaviour is clearly reflected in its food picture. Molluscs, which attach themselves firmly to the substrate, form the main part of its food. Compared with their percentage distribution in the bottom fauna, the proportion of animals of this group in the stomach contents of the grayling is extraordinarily high. There must, therefore, be a direct food preference on the part of the grayling. Such a preference is also shown by the proportion of *Coleoptera* (*Helminae*) from concealed habitats which are rarely observed in the drift and which must therefore be actively lifted from the substrate. It follows from the feeding behaviour of the grayling that the high percentage of *Simuliidae* in its stomach contents does not originate from the drift but from the bottom fauna.

These investigations are concerned only with the utilisation of the bottom

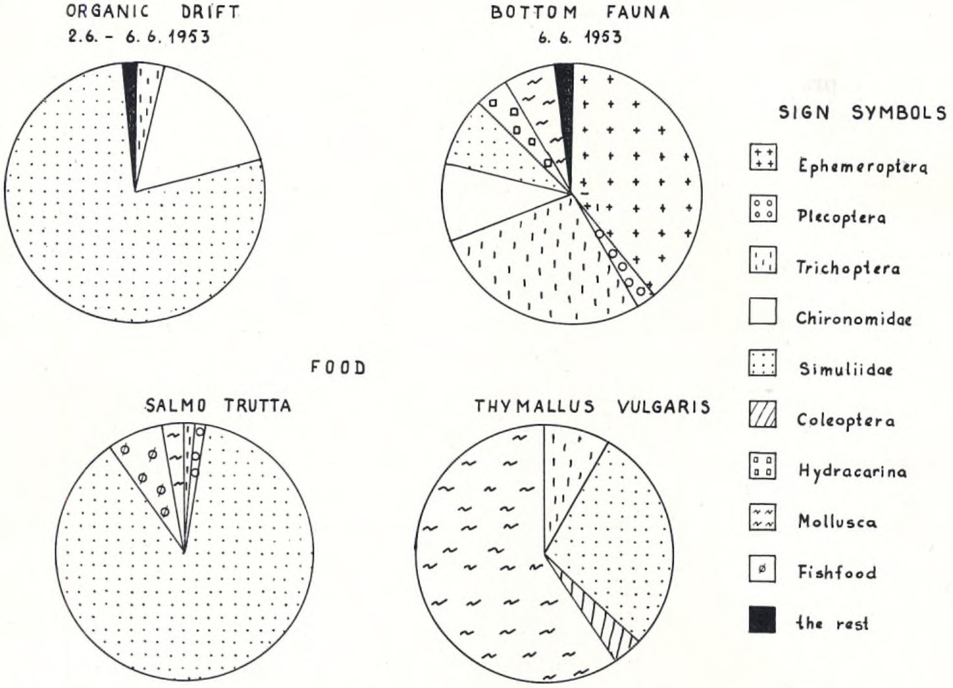

Fig. 7. Survey of drift, bottom fauna and the food uptake of *Salmo trutta* and *Thymallus vulgaris* in the lower reaches of the River Kvarnån.

fauna by the two species of fish in whose diet air-borne food still plays an insignificant role, at the beginning of June.

When we compare the food picture of the trout with that of the grayling we frequently find that the foods of the two species are, to a large extent, similar. We might therefore suppose that keen competition exists between them. The investigation described here shows, however, that competition does not occur, in spite of the overlapping of certain food components, since the origin of the food, e.g. of the Simuliid larvae, is different. The two Salmonids, therefore, inhabit quite distinct ecological niches — the trout the region of open water, the grayling the bottom region of the stream.

On account of its importance in the feeding of the trout alone, the drift plays an important part in the cycle of production in running water. To a much greater extent the drift is used by many benthic groups of animals which have a passive method of feeding (*Orthocladiinae, Simuliidae, Hydropsychidae, Neureclipsis* and other food-snaring *Trichoptera*). For these animals the presence of a drift of living and dead organic substance is a prerequisite of life.

VI. Summary

In the present work a preliminary survey is made of the phenomenon of drift in running water. The investigations carried out in the summer of 1953 in some streams in the North Swedish forest regions revealed that a drift of living organisms of the benthos took place during the whole period of the observations from May to October (1953). Nearly all the animal groups present in the waters investigated could also be shown to be components of the drift. The predominating forms were Chironomid, Simuliid, Ephemeropteran and Trichopteran larvae. *Hydracarina, Coleoptera* and *Mollusca,* on the other hand, were present only in small numbers.

The causes of the drift must be sought in the mechanical effects of the current. The spring floods, the breaking up of the ice and the very variable water levels in streams are the mechanical factors bringing about the drift.

In addition to these mechanical factors the main cause of drift formation lies in the competition between individuals. As is known, egg laying takes place in most concentrated form in particular regions. At these points a marked reduction in the food supply would take place during the period of growth in the summer months. The drift of organisms into other free habits in the stream causes distribution of the larvae. To this extent the drift is of importance in the production cycle from the point of view of population regulation.

The drift is maintained by the colonization cycle. On the basis of the various observations which have been cited and of our own findings, it may be presumed that most imagines of aquatic insects deposit their eggs above the place where their larvae are found.

Observations on the feeding habits and on stomach contents of the trout have shown that this species gets its food largely from the drift. In addition to its importance in the production cycle as a population-regulating factor, the phenomenon of drift is, therefore, also an important factor in population maintenance.

Oviposition

Drift
→ = Distribution of larvae over the whole stream —
→ *Population regulation*
→
→ = As important food components for *Salmo trutta* and all animal forms with a passive mode of feeding —
Population maintenance

Colonization cycle
involves a continuous drift.

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Produktionsbiologische Untersuchungen in Nordschwedischen Fliessgewässern

Teil: 2. Untersuchungen über Verbreitung, Bestandsdichte, Wachstum und Ernährung der Fische der Nordschwedischen Waldregion

Von KARL MÜLLER

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Vorwort

Obwohl uns durch die Arbeiten von EKMAN und HUITFELT-KAAS schon seit langem ein guter Überblick über die geographische Verbreitung der Fischfauna Skandinaviens gegeben ist, fehlen eingehendere Detailuntersuchungen in dem faunistisch wenig erschlossenem Gebiet der nordschwedischen Waldregion. Im Rahmen von fischereibiologisch-limnologischen Untersuchungen in den Jahren 1952—1954 im Gebiet um Bodträskfors (Abb.: 1) wurden der Verbreitung und der Bestandsdichte der Fischfauna, dem Wachstum und der Ernährung der Hauptnutzfische besondere Beachtung geschenkt. Die vorliegende in einem geographisch relativ eng umgrenzten Gebiet durchgeführte Untersuchung soll als Teildarstellung der im Gang befindlichen Untersuchungen im gesamten Gebiet des Lule-Älvs angesehen werden.

I. Qualitative und quantitative Untersuchungen über den Fischbestand

Die im nachfolgenden beschriebenen Untersuchungen erstreckten sich auf das in Abb.: 1 gezeigte Flussystem des Bodträskån. Dieses System mündet

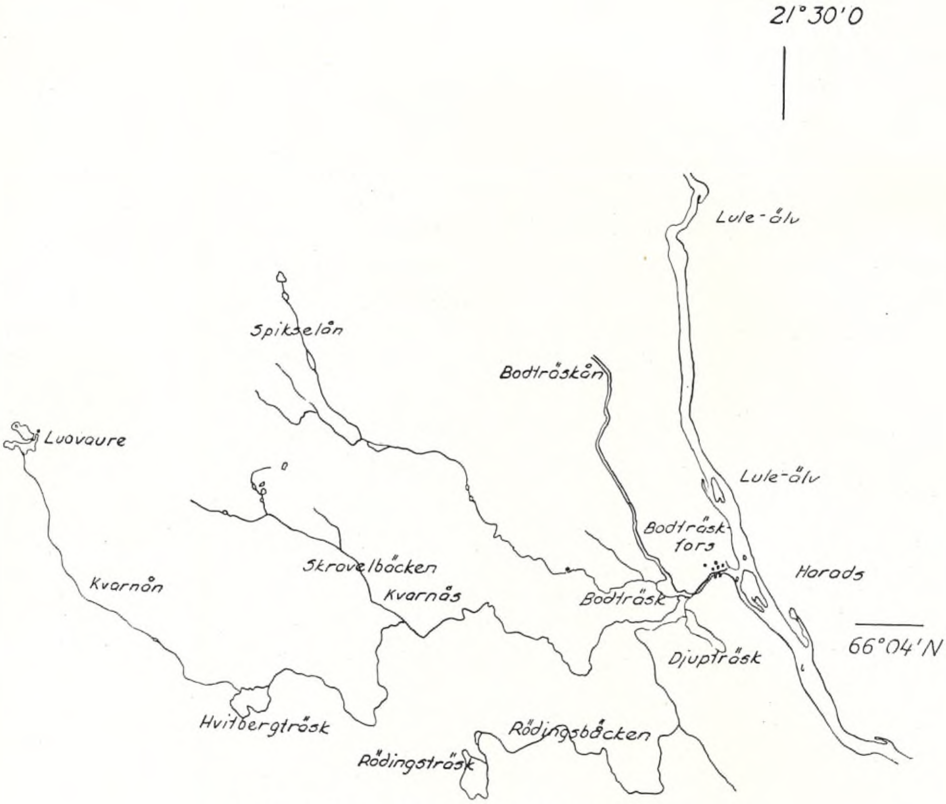

Abb.: 1 Karte des Untersuchungsgebietes.

gegenüber dem Orte Harads in den Unterlauf des Lule-Älv. Alle Flüsse durchlaufen eine wellige Moränenlandschaft und liegen meist in Bereichen unterhalb der marinen Grenze (hier etwa bei 200 m über N.N.). Das Gebiet ist vorherrschend mit Nadelwald bestanden, daneben finden sich *Betula, Salix, Alnus* und *Populus*. In Talmulden sind ausgedehnte Moorflächen bestimmend, oft findet man hier auch kleinere, flache Seen, die von den Flüssen und Bächen durchlaufen werden oder von ihnen ihren Ursprung nehmen. Über die Besonderheiten des Quelltypus und der damit verbundenen Temperaturentwicklung wurde an anderer Stelle (MÜLLER 1954) eingehender Stellung genommen.

Es handelt sich bei dem hier ausgewählten Untersuchungsgebiet um einen sehr schwach besiedelten Bereich. Einflüsse durch Abwässer u.a. Verunreinigungen liegen nicht vor. Bis vor kurzem war der natürliche Zustand der Gewässer noch voll erhalten. Erst im Jahre 1947 (Bodträskån) wurde begonnen zum Zwecke der Flösserei Regulierungen in den Fliessgewässern durchzuführen. Über die Einflüsse dieser Regulierungen auf die Bodenfauna der Gewässer wurde ein vorläufiger Bericht vorgelegt (MÜLLER 1953). Neben einer faunistisch-ökologischen Untersuchung über den Fischbestand war es im Rahmen dieser Abhandlung gleichfalls von Interesse den Einfluss der genannten Regulierungen auf den Fischbestand zu untersuchen.

Letzte Folgerung einer produktionsbiologischen Untersuchung ist die Frage nach der Ertragsfähigkeit eines Gewässers. Man bediente sich bisher mangels geeigneter anderer Methoden der Fischereistatistik. Diese Methode gibt natürlich in einem längeren Zeitraum angewandt relativ sichere Anhalte, ihr liegt aber immer die Zufälligkeit des Fanges mit dem Netz zu Grunde. Letztes Ziel muss es deshalb sein, eine Methodik anzuwenden, die eine quantitative Erfassung des Fischbestandes ermöglicht. Dass eine solche Erfassung nie vollkommen sein kann, ist verständlich. Der hier angewandten Methode des Elektrofischfanges kann aber eine Genauigkeit von 80—90 % zugesprochen werden, damit sind hinreichend genaue Beurteilungsmöglichkeiten gegeben.

Zur Bestimmung des qualitativen und quantitativen Fischbestandes einiger Wasserläufe wurden folgende Wege beschritten: Bestimmte Bachbereiche wurden auf 50—100 m mit Netzen abgesperrt und entgegen der Strömungsrichtung ausgefischt. Die Fische wurden gemessen, Schuppenproben entnommen und zum Teil für Nahrungsuntersuchungen konserviert. Auf diese Weise konnte aus einer Anzahl Stichproben ein Überblick über Artenverteilung und Menge der Fischfauna gegeben werden. Bei den Abfischungen wurde das Elektrofischgerät »Salmo Super» der Firma Atlas-Marin AB benutzt. In den Untersuchungen wurde die Länge und die Fläche der abgefischten Strecke bestimmt, somit war eine Bestimmung der Fische pro m^2 möglich. Aus diesem Zahlenwert (Fische/m^2) wurde eine Berechnung für den Fischbestand per Hektar durchgeführt.

1.) Untersuchungen über den qualitativen und quantitativen Fischbestand des Skravelbäcken.

An fünf Punkten dieses etwa 10 km langen Baches wurden quantitative Elektroabfischungen durchgeführt. Diese Untersuchungen wurden ergänzt durch Netz-, Reusen- und Angelfänge im mittleren Bachbereich (zwischen den Untersuchungen 2 und 3) und in den im Quellbereich liegenden Pesok- und Storträsk. Die Ergebnisse der Elektroabfischungen sind in der Abbildung 2 und in den Tabellen 1—5 dargestellt.

In der Abbildung 2 sind die Ergebnisse dieser Abfischungen dargestellt. Es zeigt sich, dass im Oberlauf nur *Lota vulgaris* und *Phoxinus laevis* anzutreffen sind. Diese Beobachtungen konnte vielerorts gemacht werden, in den sehr nahrungsarmen, sauren Gewässern unterhalb von ausgedehnten Sumpfgebieten konnten Salmoniden nur selten beobachtet werden. *Lota* und *Phoxinus* sind die typischen Fische solcher Bereiche, häufig tritt hierzu der aus den Seen ausgewanderte Hecht. Die Untersuchung 2 zeigt das erste

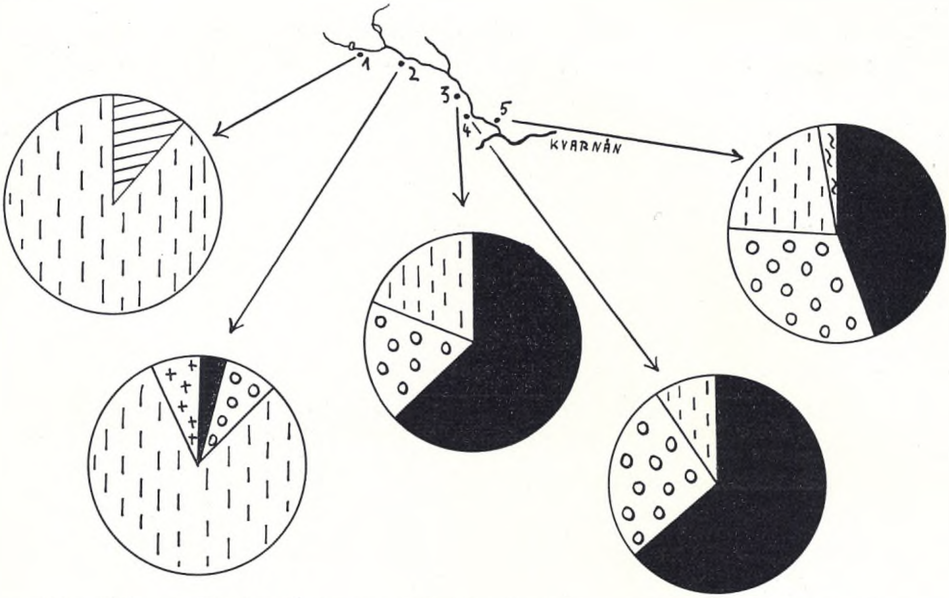

Abb.: 2 Die qualitative und quantitative Zusammensetzung des Fischbestandes im Skravelbäcken. (Zeichenerklärung in 3.)

Tab.: 1 Pesokbäcken, westlicher Quellarm des Skravelbäcken. Bachstrecke unterhalb des Pesokträsk, Bach verläuft durch dichtes *Alnus-* und *Salix* Buschwerk. Strömung 0,30—0,50 m/sec. Am Boden faustgrosse Steine mit *Batrachospermum vagum* bewachsen, starke Eisenausfällungen.

Abgefischte Strecke: .... 80 m
Abgefische Fläche: .... 60 m²

Fischart	Anzahl gefangener Fische	%-Anteil Gesamtfang	Fische m²	Fische ha
Lota vulgaris	1	11	0,15	167
Phoxinus laevis	8	89		1333

Tab.: 2 Mittellauf des Skravelbäcken bei »Skogskoja». Gefällestrecke im Anschluss an ein ausgedehntes Sumpfgebiet. Starke Eisenausfällungen, geringe Benthosbesiedlung. Srömung 0,40—0,60 m/sec.

Abgefischte Strecke: .... 50 m
Abgefischte Fläche: .... 100 m²

Fischart	Anzahl	%-Anteil Gesamtfang	Fische m²	Fische ha
Salmo trutta	1	3,8	0,26	100
Cottus gobio	2	7,7		200
Phoxinus laevis	21	80,8		2100
Esox lucius	2	7,7		200

Tab.: 3 Unterlauf des Skravelbäcken. Granitgeröll bildet den Bachgrund. Tiefer liegende Steine zeigen starken Bewuchs mit *Fontinalis*. Strömung 0,50 —0,70 m/sec.

Abgefischte Strecke: .... 60 m
Abgefischte Fläche: .... 110 m^2

Fischart	Anzahl	⁰/₀-Anteil Gesamtfang	Fische m^2	Fische ha
Salmo trutta	10	62,4	0,15	909
Cottus gobio	3	18,8		273
Phoxinus laevis	3	18,8		273

Tab.: 4 Gleicher Bachtyp wie in Tab.: 3.

Abgefischte Strecke: .... 45 m
Abgefischte Fläche: .... 100 m^2

Fischart	Anzahl	⁰/₀-Anteil Gesamtfang	Fische m^2	Fische ha
Salmo trutta	7	63,7	0,11	700
Cottus gobio	3	27,7		300
Phoxinus laevis	1	9,1		100

Tab.: 5 Unterlauf des Skravelbäcken oberhalb der Mündung des Baches in den Fluss Kvarnån. Dieser bereich wurde im Juni 1952 reguliert (gereinigt). Mit Hilfe eines Traktors wurde der Bachgrund ausgeräumt und eine glatte Bachrinne geschaffen. Kein Pflanzenwuchs. Strömung 0,50—0,80 m/sec.

Abgefischte Strecke: .... 85 m
Abgefischte Fläche .... 300 m^2

Fischart	Anzahl	⁰/₀-Anteil Gesamtfang	Fische m^2	Fische ha
Salmo trutta	17	44,7	0,13	567
Cottus gobio	12	31,6		400
Phoxinus laevis	8	21,1		267
Petromyzon planeri	1	2,6		33

Auftreten von *Salmo trutta*, vergesellschaftet mit dem *Esox, Cottus* und *Phoxinus*. Es handelt sich hier um eine kleinere Gefällestrecke zwischen zwei ausgedehnten Sumpfbereichen. Der Fischbestand in diesen tiefen mit geringer Strömungsgeschwindigkeit verlaufenden Bachabschnitten in den Sumpfstrecken wurde mit Netzen und Angelfischerei festgestellt. Es zeigte sich dabei, dass der Hecht hier ein regelmässiger Besiedler ist. Sicherlich kommt dieser Fisch aus dem im Oberlauf liegenden Storträsk der einen reichen Bestand an *Esox lucius* aufweist. Daneben findet sich auch *Salmo trutta* in grösseren Exemplaren. Für die Forelle muss sich eine solche Vergesellschaftung nachteilig auswirken. Die Erträge dieser Strecken sind demgemäss auch sehr gering. Als typischen Fischbestand der Sumpfbereiche kann man *Phoxinus laevis, Petromyzon planeri, Lota vulgaris* und *Esox lucius* ansehen, hinzu kommt *Salmo trutta* in nur geringer Häufigkeit.

Im Unterlauf des Baches dominieren die typischen Formen einer Forellenregion: *Salmo trutta, Cottus gobio* und *Phoxinus laevis,* hinzu kommt in der Untersuchung 5, *Petromyzon planeri.* Auffallend ist die weitgehende Gleichheit der Resultate der Untersuchungen 3 und 4. In beiden Fällen ist *Salmo trutta* in annährend gleichem Prozentanteil vertreten. In 5 ist ein Rückgang des Forellenbestandes festzustellen. Es liegt nahe, diese Erscheinung mit der im Jahre 1952 erfolgten Regulierung des Bachabschnittes in Zusammenhang zu bringen. Gegenüber von 3 und 4 ist hier besonders ein starker Zugang von *Cottus* festzustellen. In der Untersuchung über die Bodenfauna konnte bekanntlich gezeigt werden, dass in Folge der Regulierung ein starkes Ansteigen rheophiler Larvenformen (*Simulium*) festzustellen war. *Cottus* als Bodenfisch lebt aber in wesentlich höherem Umfange von Bodentiernahrung als die Forelle, die ja besonders in den Sommermonaten die Luftnahrung ausnützen kann. Es liegt die Vermutung nahe, dass hier eine Veränderung des Fischbestandes zum Nachteil der Forelle erfolgte, d.h. dass durch die Milieuveränderung die Lebensbedingungen für die Art *Cottus gobio* wesentlich verbessert wurden. An anderer Stelle (MÜLLER 1952) wurde auf die Konkurrenz von Koppe und Forelle bereits verwiesen. Es konnte dabei gezeigt werden, dass *Cottus* in vielen Nahrungskomponenten mit der Forelle übereinstimmt, ein starker Koppenbestand muss sich also besonders unter verbesserten Lebensbedingungen für den Fisch zum Nachteil der Forelle auswirken. Es liegt nahe in dem vorliegenden Falle eine solche Deutung des verminderten Forellenanteils zu suchen.

Neben einer Bestandsaufnahme der Fischfauna ist es ja unter fischereibiologischen Gesichtspunkten wichtig zu wissen in welcher Altersklassenverteilung die Fische auftreten. In der Untersuchung 2 wurde eine Forelle gefangen die mit 24 cm Länge (Lt) zur Altersklasse III gehörte. Für die Untersuchungen 3, 4 und 5 zeigte sich folgende Verteilung:

Tab.: 6 Die Altersklassenverteilung in Untersuchung 3.

Fischart	Anzahl	Variationsbreite Länge (Lt) cm	Altersgruppe	%
Salmo trutta	8	8—12	I	62
» »	4	16—18	II	31
» »	1	23	III	7

Tab.: 7 Die Altersklassenverteilung in Untersuchung 4.

Fischart	Anzahl	Variationsbreite Länge (Lt) cm	Altersgruppe	%
Salmo trutta	3	9—11	I	42
» »	2	15—18	II	29
» »	2	21—24	III	29

Tab.: 8 Die Altersklassenverteilung in Untersuchung 5.

Fischart	Anzahl	Variationsbreite Länge (Lt) cm	Altersgruppe	%
Salmo trutta	14	8—12	I	82
» »	2	16—18	II	12
» »	1	22	III	6

Auf Grund des geringen Untersuchungsmaterials ist eine Beurteilung nur schwierig. Auffallend ist jedoch der hohe Anteil der Altersgruppe I in der Untersuchung 5. Wie schon weiter oben erwähnt handelt es sich hierbei um den regulierten Abschnitt im Unterlauf des Baches. Die Regulierung beseitigt alle grösseren Steine und schafft eine glatte Bachrinne. Für grössere Fische sind die Aufenthaltsorte begrenzt, jungen Fischen sind aber durch das hohe Nahrungsangebot günstige Lebensbedingungen gegeben.

2. Untersuchungen über den qualitativen und quantitativen Fischbestand im Spikselån.

Die Untersuchungen im Flusse Spikselån zeigen in vieler Hinsicht ein gleiches Bild wie es im Skravelbäcken beobachtet werden konnte. Ein qualitativer Unterschied besteht lediglich im Auftreten der Äsche (*Thymallus vulgaris*).

In seinem Verlauf durchfliesst der Fluss verschiedene Seen. Der östliche Quellarm nimmt seinen Ursprung in einem grösseren nahezu ausschliesslich mit Barsch (*Perca fluviatilis*) besiedelten See. Im Mittelauf des östlichen Quellaufes wird der Långträsk durchflossen. Dieser See hat einen gemischten Fischbestand bestehend aus: Barsch (*Perca fluviatilis*), Plötze (*Leuciscus rutilus*), Hecht (*Esox lucius*) und vereinzelten Forellen (*Salmo trutta*).

Der westliche Quellarm kommt aus einem ausgedehnten Sumpfgebiet, ein deutlicher Bachlauf ist erst beim Zusammenfluss der beiden westlichen Quellzuflüsse zu erkennen. *Lota vulgaris* war hier der Fisch, der am weitesten flussaufwärts verbreitet war. Der westliche Quellbereich besteht aus einer grossen Anzahl von Helokrenen die ihr Wasser in flachen Moortümpeln sammeln. Zwischen den Moortümpeln besteht dann meist eine Verbindung durch ein kleines Rinnsal. Bis in diese Bereiche stieg *Lota* auf, andere Fischbesiedlung konnte hier nicht nachgewiesen werden.

Wenig oberhalb des Tekakott-Träsk fliessen der östliche und westliche Quellarm zusammen. Der See selbst ist ca 2 km lang und durchschnittlich 200—300 m breit. Seine grösste Tiefe liegt bei 12 m. Er zeigt das Bild eines typischen Waldsees, mit starker *Phragmites* und *Equisetum* Vegetation in der Strandzone. Der Ufervegetation vorgelagert ist ein dichter Gürtel, mit *Potamogeton* und *Nuphar luteum* und *Nymphea candida*. In der Freiwasserzone zeigte sich in verschiedenen Untersuchungen eine reiche Planktonentwicklung. Die Hauptformen des Zoo- und Phytoplanktons waren: *Sida cristallina, Bosmina spec., Acropus harpae, Dahpnia spec., Polyphemus pediculus, Polyarthra spec., Kelikothia longispina, Cyclops spec., Tabellaria floculosa* und *Eunotia pectinalis.*

Um eine Übersicht über den Fischbestand dieses Sees zu gewinnen, wurden mit Netzen verschiedener Maschenweiten Probeabfischungen durchgeführt. Die im September 1952 und September 1953 durchgeführten Abfischungen zeigten folgende Zusammensetzung der Fischfauna:

	Anzahl	⁰/₀
Leuciscus rutilus	2450	=68
Perca fluviatilis	780	=22
Esox lucius	210	= 6
Lota vulgaris	70	= 2
Acarina cernua	30	= 1
Thymallus vulgaris	24	= 1

Auffallend ist das starke Überwiegen der Plötze. Es zeigt sich hier im Tekakott-Träsk ein Bild das typisch für viele schwedischen Seen ist. Mangelnde Befischungsintensität und teilweise einseitige Befischung (Raubfische, grosse Maschenweiten) führen zu einer Übervölkerung mit einer zur Massenvermehrung neigenden Fischart. An anderer Stelle dieser Ausführungen konnte an Hand des Wachstums der Plötzenpopulation des Tekakott-Träsk die Richtigkeit der hier angestellten Überlegung bewiesen werden.

Unterhalb des Sees durchfliesst der Spikselån verschiedene Gefällebereiche, durchläuft zwischen den Untersuchungen 4 und 5 zwei kleine Seen, die den gleichen Fischbestand wie der Tekakott-Träsk aufweisen. Bei 5 beginnt die Regulierung des Spikselån für Zwecke der Flösserei. Die Untersuchungen 5, 6 und 7 sind regulierte Flussabschnitte, die Untersuchung 7 wurde in einem zwischen den Regulierungen liegenden natürlichen Bereich durchgeführt.

Bevor das Flussystem des Bodträskån in den Lule-Älv ausmündet, vereinigt sich das Wasser aller Flüsse und Bäche in dem See Bodträsket. Auch hier wurden umfangreiche Probeabfischungen durchgeführt. Aus einem Gesamtmaterial von ca 8000 Fischen ergab sich die in Abb.: 3 dargestellte Verteilung. Das Vorherrschen der Plözte ist hier noch mehr betont als es im Tekakott-Träsk der Fall war. Es ist aber trozt des grossen Materials schwer möglich eine Aussage zu treffen, ob das Fangresultat wirklich der natürlichen Ver-

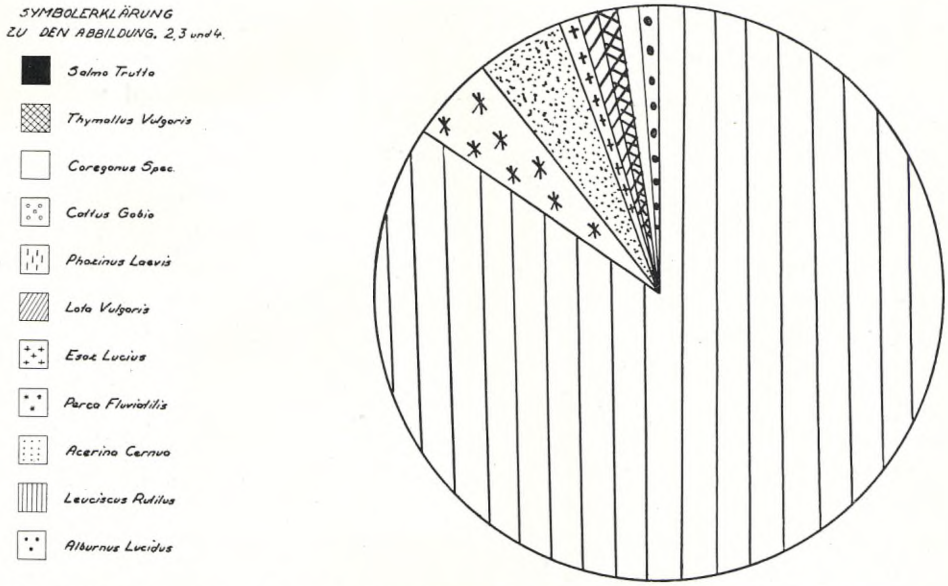

Abb.: 3 Die Zusammensetzung des Fischbestandes im Bodträsket (Nach Probeabfischungen mit Netzen verschiedener Maschenweiten).

teilung entspricht. Bei Netzfängen kann ja der Zufall, bestimmte Wanderbewegungen bestimmter Fische, den Anteil einer Art unnatürlich erhöhen oder erniedrigen. Die Erfahrungen der Fischer dieses Bereiches sprechen aber dafür, dass das hier dargestellte Verteilungsbild, der Wirklichkeit sehr nahe kommt. Zu anderen Zeiten als in den hier gleichfalls im September durchgeführten Probeabfischungen konnten *Leuciscus idus* zur Laichzeit im Juni, *Salmo trutta* (Wanderform, Meerforelle) während des Aufstiegs zu den Laichplätzen (Juni, Juli) und am 19.X.1953 ein 82 cm langes Lachsweibchen ebenfalls beim Aufstieg angetroffen werden.

Nach einer notwendigen Behandlung über das Vorkommen und die Verbreitung der Fische in den vom Flusse Spikselån berührten Gewässern, soll nun die Fischfauna der fliessenden Gewässerbereiche eingehender behandelt werden. Neben den Tabellen 9 bis 16 ist in Abb.: 4 eine Übersicht über die Fischfauna des Flusses gegeben.

Tab.: 9 Beginn des Bachlaufes unterhalb des »Pelgavare Myr». Mooriger Bachgrund. Strömung 0,40—0,60 m/sec.

Datum der Untersuchung: 18.9.53
Abgefischte Strecke: .... 90 m
Abgefischte Fläche: .... 140 m²

Fischart	Anzahl	%-Anteil Gesamtfang	Fische/m²	Fische/ha
Lota vulgaris	2	20	0,07	143
Phoxinus laevis	8	80		571

Tab.: 10 Oberhalb Tekakott-Träsk. Der Bachgrund ist mit grobem Granitgeröll bedeckt. Strömung 0,30—0,50 m/sec. Beiderseits des Baches urwaldartiger *Alnus, Salix, Betula*-wald.

Datum der Untersuchung: 18.9.53
Abgefischte Strecke: .... 60 m
Abgefischte Fläche: .... 130 m²

Fischart	Anzahl	%-Anteil Gesamtfang	Fische/m²	Fische/ha
Salmo trutta	2	13		154
Cottus gobio	4	27		308
Phoxinus laevis	7	47		538
Esox lucius	2	13	0,12	154

Tab.: 11 Unterhalb Tekakott-Träsk. Grosse Steinblöcke bedecken unregelmässig den Bachgrund. Bereiche starker Strömung (0,80—1,00 m/sec) wechseln mit schwacher Strömung (0,40—0,50 m/sec). Nur geringer submerser Pflanzenwuchs.

Datum der Untersuchung: 12.8.52
Abgefischte Strecke: .... 150 m
Abgefischte Fläche: .... 850 m²

Fischart	Anzahl	%-Anteil Gesamtfang	Fische/m²	Fische/ha
Salmo trutta	1	2	0,08	12
Thymallus vulgaris	2	3		24
Cottus gobio	12	18		141
Phoxinus laevis	47	72		553
Lota vulgaris	2	3		24
Esox lucius	1	2		12

Tab.: 12 Oberhalb Spikbergträsk. Gleiches Bachbild wie in Tab.: 11.

Datum der Untersuchung 13.7.53
Abgefischte Strecke: .... 45 m
Abgefischte Fläche: .... 405 m²

Fischart	Anzahl	%-Anteil Gesamtfang	Fische/m²	Fische/ha
Salmo trutta	2	2	0,21	49
Thymallus vulgaris	4	5		99
Cottus gobio	7	8		173
Phoxinus laevis	66	78		1630
Esox lucius	2	2		49
Lota vulgaris	4	5		99

Tab.: 13 Unterhalb Spikberg-Träsk. Dieser Bereich wurde im Sommer 1951 reguliert.

Datum der Untersuchung: 12.8.53
Abgefischte Strecke: .... 130 m
Abgefischte Fläche: .... 420 m²

Fischart	Anzahl	%-Anteil Gesamtfang	Fische/m²	Fische/ha
Salmo trutta	4	9	0,12	95
Thymallus vulgaris	3	6		71
Cottus gobio	15	32		357
Phoxinus laevis	25	53		595

Tab.: 14. Regulierter Flussbereich bei »Vidselbrücke», im Gegensatz zu der in Tab.: 13 dargestellten Untersuchung besteht hier der Flussgrund aus kleinem bis zu faustgrossen Steinmaterial und Kies. Strömungsgeschwindigkeit 0,60—0,80 m/sec.

Datum der Untersuchung: 18.7.53
Abgefischte Bachstrecke: .... 75 m
Abgefischte Wasserfläche: .... 360 m²

Fischart	Anzahl	%-Anteil Gesamtfang	Fische/m²	Fische/ha
Salmo trutta	30	36	0,23	833
Cottus gobio	35	42		972
Phoxinus laevis	18	22		500

Tab.: 15 Untersuchung unweit des Gehöftes »Spikselå». Natürlicher Bachbereich. Bachbett tief erodiert. Bachgrund besteht aus Kies und Sand, dazwischen vereinzelte grössere Steinblöcke. Strömungsgeschwindigkeit 0,30 —0,50 m/sec.

Datum der Untersuchung: 23.9.53
Abgefischte Strecke: .... 50 m
Abgefischte Fläche: .... 200 m²

Fischart	Anzahl	%-Anteil Gesamtfang	Fische/m²	Fische/ha
Thymallus vulgaris	3	11	0,13	150
Cottus gobio	2	8		100
Phoxinus laevis	15	57		750
Lota vulgaris	2	8		100
Esox lucius	2	8		100
Petromyzon planeri	2	8		100

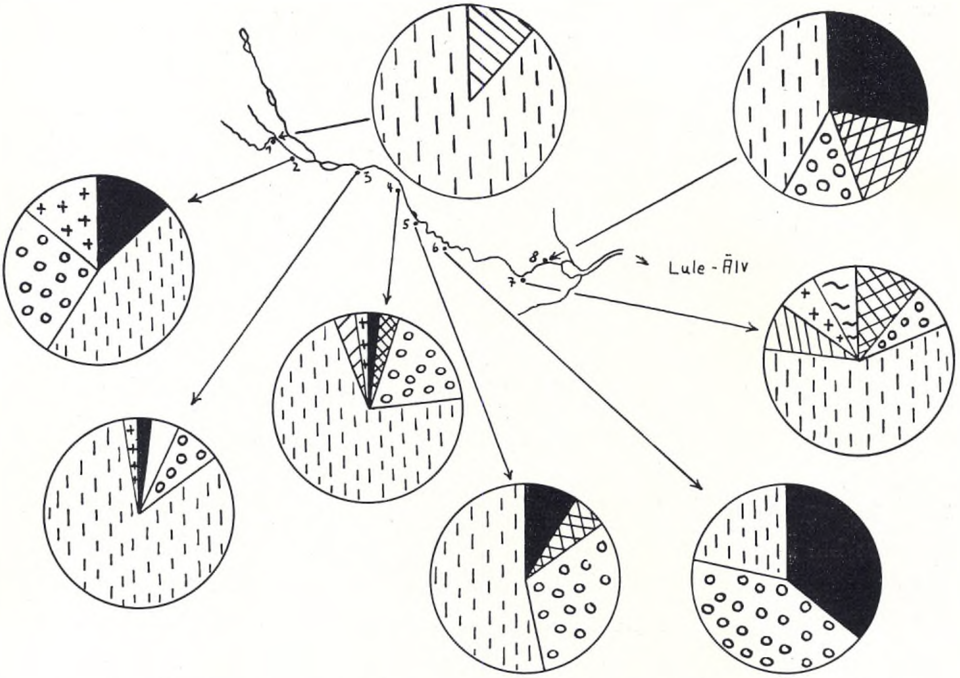

Abb.: 4 Die qualitative und quantitative Zusammensetzung des Fischbestandes im Spikselån. (Zeichenerklärung in 3.)

Tab.: 16 Bereich des Spikselån oberhalb der Einmündung des Lerbäcken. Der Flussabschnitt wurde 1951 reguliert und weist etwa die gleichen Verhältnisse wie die Untersuchung »Videelbrücke» auf.

Datum der Untersuchung: 18.9.53
Abgefischte Strecke: .... 60 m
Abgefischte Fläche. .... 240 m²

Fischart	Anzahl	%-Anteil Gesamtfang	Fische/m²	Fische/ha
Salmo trutta	8	28	0,12	333
Thymallus vulgaris	5	17		208
Cottus gobio	4	14		167
Phoxinus laevis	12	41		500

Die Alterklassenverteilung des dominierenden Salmoniden *Salmo trutta* ist in der folgenden Übersicht dargestellt.

Untersuchung II	2 *Salmo trutta*	16,17 cm	Altersgruppe II
Untersuchung III	1 *Salmo trutta*	10 cm	Altersgruppe I
Untersuchung IV	2 *Salmo trutta*	22,24 cm	Altersgruppe III
Untersuchung V	2 *Salmo trutta*	10,12 cm	Altersgruppe I
	1 » »	15 cm	Altersgruppe II
	1 » »	24 cm	Altersgruppe III

Untersuchung VI

Fischart	*Anzahl*	Variationsbreite Länge (Lt) cm	Altersgruppe	%-Anteil
Salmo trutta	22	8,5—13,0	I	73
» »	6	15,0—19,0	II	20
» »	2	22,0—23,0	III	7

Untersuchung VIII

Fischart	*Anzahl*	Variationsbreite Länge (Lt) cm	Altersgruppe	%-Anteil
Salmo trutta	5	10,0—12,0	I	63
» »	2	16,0—18,0	II	25
» »	1	21,0	III	12

3.) Untersuchungen über den qualitativen und quantitativen Fischbestand in verschieden kleineren Gewässern des Bodträskån — Flussystems.

Neben den Elektroabfischungen die das Ziel hatten einen arten- und mengenmässigen Überblick über die Fischfauna einiger Gewässers in ihren verschiedenen Bereichen zu geben, wurden in verschiedenen kleineren Bächen Stichprobenuntersuchungen durchgeführt. Bei diesen Gewässern handelt es sich um kleine meist nur 3—5 km lange Waldbäche. Ihren Ursprung nehmen diese Bäche aus kleineren Seen. Die Wasserführung und Temperatur ist in diesen Gewässern während des gesamten Jahres sehr konstant. Fast alle Bäche mit Ausnahme des Unterlaufes des Rödingstjärnbäckens, weisen eine ausserordentlich reiche Bodenfauna auf. Wie besonders die Beispiele Mörtträskbäcken und Björnbergsträskbäcken zeigen, ist der Fischbestand dieser Gewässer im Vergleich zu dem Spikselån wesentlich besser. Auf die Ursachen der unterschiedlichen Besiedlung soll später näher eingegangen werden.

Tab.: 17 Untersuchung: *Mörtträskbäcken.* Kleiner Waldbach von durchschnittlich 0,80—1,00 m Breite. Mündet unterhalb Krogfors in den Bodenträskån. Strömung ca 0,60—0,80 m/sec. Bachgrund meist Kies und kleinere Steine. Stellenweise submerser Pflanzenwuchs (*Potamogeton*).

Datum der Untersuchung: 30.7.1953
Abgefischte Strecke: .... 140 m
Wasserfläche: .... 120 m²

Fischart	Anzahl	%-Anteil Gesamtfang	Besiedlung pro/m²	Fische/ha
Salmo trutta	11	69	0,13	917
Phoxinus laevis	3	19		250
Lota vulgaris	2	12		167

Tab.: 18 Untersuchung: *Tallbergsbäcken.* Kleiner Waldbach, mündet in Spikberg-Träsk. Durchläuft in seinem Oberlauf vier Seen, gute Nahrungsbedingungen, reiches Benthos, stark befischt.

Datum der Untersuchung:	12.8.1953
Abgefischte Strecke:	95 m
Wasserfläche:	90 m²

Fischart	Anzahl	%-Anteil Gesamtfang	Besiedlung pro/m²	Fische/ha
Cottus gobio	6	100	0,07	667

Tab.: 19 Untersuchung: *Rödingstjärnbäcken.* Kleiner Waldbach, sandiger Bodengrund. Strömunggeschwindigkeit am Untersuchungsplatz 0,30—0,50 m/sec. Geringe Bodenbesiedlung.

Datum der Untersuchung:	30.7.1953
Abgefischte Strecke:	65 m
Wasserfläche:	65 m²

Fischart	Anzahl	%-Anteil Gesamtfang	Besiedlung pro/m²	Fische/ha
Phoxinus laevis	8	100	0,12	1231

Tab.: 20 Untersuchung: *Björnbergsträskbäcken.* Die Untersuchung wurde ca 1 km unterhalb des Ausflusses dieses kleinen Waldbaches aus dem ca 60 ha grossen Björnbergsträsk durchgeführt. Bachgrund besteht aus Sand und Kies, geringer Pflanzenbewuchs. Sehr reiche Bodenfauna.

Datum der Untersuchung:	12.7.1953
Abgefischte Strecke:	110 m
Wasserfläche:	200 m²

Fischart	Anzahl	%-Anteil Gesamtfang	Besiedlung pro/m²	Fische/ha
Salmo fontinalis	14	20	0,35	700
Salmo trutta	3	4		150
Thymallus vulgaris	3	4		150
Cottus gobio	12	18		600
Phoxinus laevis	28	41		1400
Lota vulgaris	1	1		50
Perca fluviatilis	8	12		400

4.) Untersuchungen über den Fischbestand in verschiedenen Seen.

Bei der Beschreibung der Fische des Flusses Spikselån war schon eingehender auf den Fischbestand der vom Fluss durchflossenen Seen eingegangen worden. Es war nun in jedem einzelnen Falle nicht möglich durch umfassende Probeabfischungen einen Anhalt über den Fischbestand zu geben. Jedoch wurden in einer Vielzahl von Seen Stichprobenuntersuchungen durchgeführt und es erscheint wertvoll in einer Zusammenfassung über die Fischfauna des Gebietes um Bodträskfors auch diese Resultate darzustellen.

Zunächst muss festgestellt werden, dass in diesem Gebiet, besonders im Oberlauf des Flusses Bodträskån und des Skravelbäcken noch eine Reihe von Seen ohne jeglichen Fischbestand sind. Diese Seen haben sich beim Abschmelzen des Eises gebildet (Ablationsmoränen, »dödismorän»). Eine direkte Verbindung mit einem Fliessgewässer besteht in den seltensten Fällen, meist ist aber ein unterirdischer Ausfluss vorhanden. In anderen Fällen war durch steilabfallende Seeausflüsse eine Besiedlung ebenfalls ausgeschaltet. Es kann daher für viele heute bevölkerter Seen angenommen werden, dass eine Besiedlung durch den Menschen erfolgte. Nur unter dieser Voraussetzung lassen sich einige tiergeographisch unverständliche Zusammensetzungen der Fischfauna erklären.

a.) *Der Fischbestand der Seen im Einzugsgebiet des Skravelbäcken.*

Wie aus der Kartenskizze in Abbildung 1 zu ersehen ist nimmt der Bach seinen Ursprung in zwei kleinen Seen, dem westlichen »Pesokträsk» und dem östlichen »Storträsk». Im »Pesokträsk» wurden beobachtet: *Perca fluviatilis, Leuciscus rutilus, Lota vulgaris* und *Phoxinus laevis.* Im »Storträsk»: *Salmo trutta, Esox lucius, Phoxinus laevis, Lota vulgaris.* In dem etwa 6 ha grossen oberhalb des Quellsumpfes gelegenen »Björnbergstjärn» war bis zum Jahre 1947 nach Aussagen der ortseingesessenen Bevölkerung keine Fischbesiedlung. 1947 wurden *Salmo trutta* und *Thymallus vulgaris* implantiert. Beide Fische haben sich sehr gut enwickelt und es wurden auf Grund der Fangregistrierungen im Jahre 1953 ca 150 Fische gefangen, da nur Netzfänge registriert wurden lag der tatsächliche Ertrag sicherlich höher. Im Mittellauf des Baches liegt in etwa 2 km Abstand vom Bach ein kleiner ca 4 ha grosser Waldsee der einen ausschliesslichen Bestand sehr schlechtwüchsiger Barsche aufweist (»Abborretjärn»).

b.) *Der Fischbestand der Seen im Einzugsgebiet des Flusses Kvarnån.*

Der Fluss kommt aus dem See Luovaure, in diesem See wurden 1952 und 1953 umfangreichere Probeabfischungen durchgeführt. Hier, sowie in dem einige Kilometer unterhalb durchflossenen Hvitbergsträsk ist nahezu der gleiche Fischbestand anzutreffen wie er in Abb.: 3 im Bodträsket dargestellt wurde. Es dominieren *Leuciscus rutilus* und *Perca fluviatilis,* mit Abstand folgen: *Esox lucius, Acerina cernua, Lota vulgaris, Salmo trutta* und *Thymallus vulgaris.* Im Luovaure wurden 1947 *Anguilla vulgaris* und 1950 *Coregonus spec.* implantiert, beide Fischarten wurden bisher nicht wiedergefangen.

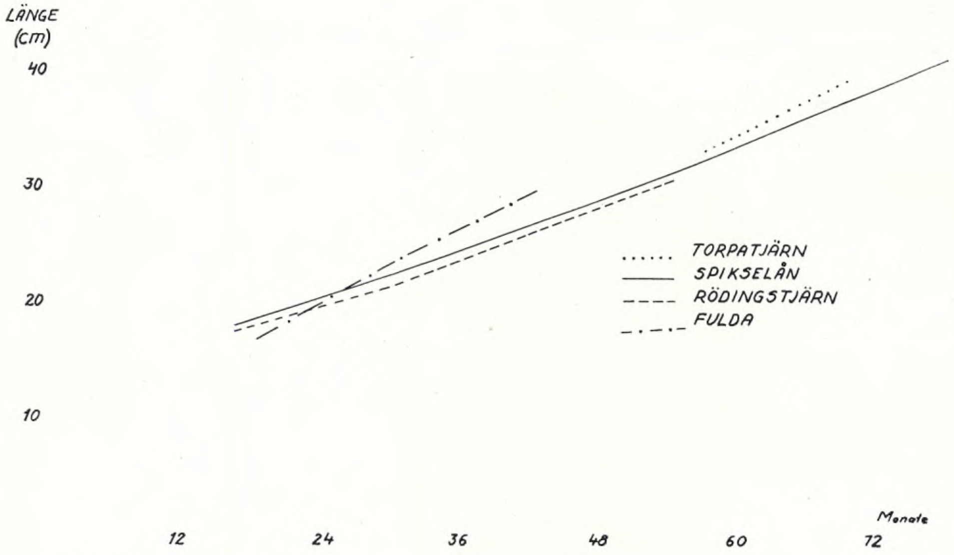

Abb.: 5 Das Wachstum verschiedener Forellenpopulationen.

Oberhalb der Einmündung des Skravelbäckens liegt der abflusslose Torpatjärn. Im Herbst 1952 konnte die 1947 und 1948 implantierte Brut (*Salmo trutta*) in 10 Exemplaren wiedergefangen werden. Der Zuwachs dieser Fische ist aus Tabelle 22 und Abb.: 5 zu ersehen.

Im Mittelauf des Flusses Kvarnån wurden 1950 einsömmerige Bachsaiblinge implantiert. Wiederfänge im Fluss konnten nicht festgestellt werden. Zum Verbleib dieser Fische konnten interessante Beobachtungen angestellt werden. Parallel zum Skravelbäcken münden östlich des Baches in den Fluss Kvarnån die kleinen Bäche »Rödingstjärnbäcken» und »Björnbergsträskbäcken». Die Elektroabfischungen in dem letztgenannten Bach (Vergl. Tab.: 20) zeigten, dass unter den Salmoniden — *Salmo fontinalis*-dominierte. Hier wie in dem benachbarten »Rödingstjärnbäcken» konnte beobachtet werden, dass die in dem Hauptfluss implantierten Fische die kleineren, kälteren Bäche aufsuchen. Im Falle des »Rödingstjärnbäckens» konnte darüberhinaus festgestellt werden, dass *Salmo fontinalis* 5 km aufwärts in den kalten in ca 300 m über NN liegenden Rödingstjärn aufgewandert war. Dieser See hatte bisher einen reinen Forellenbestand. Der kontrollierbare Ertrag dieses nur etwa 3 ha grossen Waldsees war nach den Aufzeichnungen des Fischers sehr gut. Danach wurden in der Periode von September 1952 bis Juni 1953 240 Forellen gefangen. Erstmalig waren im Frühjahr 1953, 1 *Salmo fontinalis* unter den Fängen. Da die hier beobachteten Saiblinge und die im »Björnbergträskbäcken» der gleichen Altersgruppe angehörten, liegt die Annahme des gleichen Ursprungs nahe.

c.) *Der Fischbestand der Seen im Einzugsgebiet des Spikselån.*

Der Fischbestand der in unmittelbarer Verbindung mit dem Flusse stehenden Seen war weiter oben schon näher behandelt worden. Der Fischbestand anderer mit dem Fluss in Verbindung stehender Seen unterscheidet sich nur geringfügig von der Zusammensetzung der Fischfauna wie sie im Beispiel des Tekakott-Träsk dargestellt wurde. So hat der 2 km nördlich des Tekakott-Träsk liegende »Hattjärn» in *Leuciscus rutilus* und *Perca fluviatilis* die dominierenden Formen. Anders ist die in den vier Seen die von dem »Tallbergsbäcken» durchflossen werden. Alle vier Seen haben einen reinen Barschbestand. Eine 1950 erfolgte Implantierung von Coregonenbrut zeigte verständlicherweise kein Resultat. Demgegenüber haben sich Implantierungen von einsömmerigen *Salmo fontinalis* in dem »Mörttjärn» im Jahre 1948 ausserordentlich gut entwickelt.

d.) *Der Fischbestand der Seen im Einzugsgebiet des Flusses Bodträskån.*

Im Oberlauf dieses Flusses liegt der grösste See des gesamten Bodträskforsbereiches — der Holmträsk. Hier wurde vor 50—60 Jahren noch mit dem Zugnetz gefischt. Der Hauptnutzfisch war zu dieser Zeit *Coregonus spec.* Heute sind *Leuciscus rutilus* und *Perca fluviatilis* die Hauptformen. Die Zusammensetzung des Fischbestandes wie sie in der Abbildung 3 gezeigt wurde ist für alle Seen des Bereiches Holmträsk — Puttaure zutreffend — der fischereiliche Nutzungswert ist gering.

e.) *Der Fischbestand der Seen im Einzugsgebiet des Rödingsträskbäcken.*

Der Quellsee dieses Flusses war Gegenstand einer besonderen Untersuchung (Vergl. MÜLLER 1954 d). Hier liegen besondere Verhältnisse vor, vor allem weicht die Gestaltung des Seebeckens grundsätzlich von allen anderen Seen ab. Während alle anderen bisher behandelten Seen eine ungefähre mittlere Tiefe von 8—15 m aufweisen, ist der Rödingsträsk an seinem tiefsten Punkt nur 4 m tief. Die mittlere Tiefe liegt bei 2,0—2,5 m. Nach Aussagen der Bevölkerung hatte der See früher (etwa um die Jahrhundertwende) einen guten *Coregonen*-bestand. *Coregonus* ist heute völlig verschwunden. An die Stelle dieses Fisches ist der 1944 implantierte Bachsaibling (*Salmo fontinalis*) getreten. Neben dem Salmoniden finden sich noch *Leuciscus rutilus* und *Gasterosteus pungitius*. Wegen der Ursachen die das Verschwinden der Maränen bedingen wird auf die obengenannte Publikation verwiesen. Im Unterlauf des Rödingsträskbäckens liegt der »Djupträsk», sein Fischbestand unterscheidet sich nicht von dem mit ihm Verbindung stehenden Bodträsket (Vergl.: Abb.: 3).

II. Untersuchungen über das Wachstum einiger Fische des nordschwedischen Waldgebietes

Zur Einordnung des Fisches in den Produktionszyklus eines Gewässers sind Untersuchungen über das Wachstum der einzelnen den Lebensraum besiedelnden Fischarten von grosser Wichtigkeit. Der Fisch als »Produktionsendglied» gibt in der Lebensäusserung des Wachstums relativ klare Aussagen über den Zustand des Gewässers. Dies kann besonders für das abgeschlossene System eines Sees verallgemeinert werden. In der fischereilichen Literatur findet man ein grosse Zahl von Untersuchungen über das Wachstum verschiedener Arten aus den verschiedensten geographischen Breiten. Dabei zeigt sich, dass das Wachstum einzelner Arten in verschiedenen Wohngewässern sehr stark differieren kann. Meist werden Differenzen mit dem verschiedenen Eutrophiegrad der zu verkleichenden Gewässer erklärt. Nur aus der Besiedlung der Bodenregion mit Nahrungstieren und der Planktondichte allein ein variierendes Wachstum einer Art zu erklären ist unvollkommen. Die wesentliche Frage der Bestandsdichte bleibt dabei nicht behandelt. In diesem Zusammenhange kann der Beitrag von SVÄRDSON (1954) als wertvoll angesehen werden, indem an Hand eines umfassenden Untersuchungsmaterials die wesentliche Rolle der Bestandsdichte als Wachstumsregulator gezeigt wird. Betrachten wir aber die Bestimmung des Wachstums als einen Schritt auf dem Wege klarer Unterlagen zur Ertragsberechnung eines Gewässers — so können wir nicht einseitig nur einen Faktor behandeln. Grundsätzlich wird erst dann eine deutliche Antwort auf die Frage der Ertragsfähigkeit eines Gewässers möglich sein, wenn Untersuchungen der Limnologie (im umfassensten Sinne) mit solchen der Bestimmung der Bestandsdichte der Fische in einem Gewässer Hand in Hand gehen. Dabei ist allerdings zu bedenken, dass uns eine Methode der Bestimmung der Bestandsdichte in einem Gewässer — vorallem ist hierbei an Seen gedacht — noch fehlt. Nur eine weitere Entwicklung der Echolotung wird hier zu Ergebnissen führen.

Abweichend von den Bedingungen in einem geschlossenen Seesystem sind die Verhältnisse in einem Fliessgewässer. Hier kann der rein limnologischen Untersuchung allein schon eine wesentliche Bedeutung zukommen. Auf eine Verschlechterung der Lebensvoraussetzungen, sei es eine Verschlechterung der Wasserqualität, Auftreten von überlegenen Konkurrenten oder Feinden (z.B. *Salmo trutta* — *Esox lucius*) oder eine Steigerung der Bestandsdichte, kann der Fisch immer so reagieren, dass er durch Wanderung ausweicht. (Vergl. MÜLLER 1954 b).

Wir müssen also bei der Beurteilung des Wachstums in einem See und in einem Fliessgewässer von verschiedenen Voraussetzungen ausgehen. Im Falle des Sees muss die Altersbestimmung und Wachstumsanalyse in erster Linie durch die Bestandsanalyse ergänzt werden, eine Komplettierung dieser Resultate durch Angaben über den Bestand der Bodenfauna, Planktondichte, und eine Registrierung der physiographischen Daten ist darüber hinaus erstrebenswert.

Bei einem Fluss oder Bach wird schon aus der Bestimmung des über einen längeren Zeitraum kontrollierten Bestandes der Bodenfauna (eine einmalige Untersuchung, kann hierbei bei den starken durch die Flugzeiten bedingten Fluktuation zu missweisenden Werten führen) und der Drift eine Aussage über Wachstum und Ertrag möglich sein. Hierbei sollte natürlich ebenfalls bei der relativ leichten Möglichkeit der Bestandsuntersuchung mit Hilfe des Elektrogerätes, diese unbedingt durchgeführt werden.

Für die hier behandelten Fliessgewässer wurden die beiden genannten Wege beschritten, die praktischen Folgerungen sollen am Schluss dieses Kapitels eingehender erörtert werden. Aus einigen von Bächen durchlaufenen Seen und einem isolierten See sollen gleichfalls Ergebnisse von Wachstumsuntersuchungen mitgeteilt werden.

1.) Das Wachstum der Forelle (*Salmo trutta*).

Wachstumsuntersuchungen an dieser Art wurden an Fischen aus dem Kvarnån, Spikselån und Skravelbäcken durchgeführt, da im Wachstum keinerlei Differenzen zu erkennen waren, wurden die Forellen aus fliessenden Gewässern zusammengefasst. Ein geringes Material stand aus einem völlig isolierten ca. 6 ha grossen See (Torpatjärn) zur Verfügung. Weiterhin wurden Forellen aus einem in einem kleinen Bach ausmündenden See (Rödingstjärn) untersucht.

Tab.: 21 Das Wachstum der Forelle (*Salmo trutta*) in fliessenden Gewässern.

Anzahl untersuchter Fische	Alter in Monaten [1]	Mittelwert cm (Lt)	Variationsbreite cm
16	18	17.8	17,5—19,0
14	30	22,4	20,5—24,0
11	42	26,6	25,0—28,0
9	54	31,0	28,0—32,0
5	66	38,0	36,0—39,5
2	78	41,0	40,0—42,0

[1] Alter in Monaten, jeweils gerechnet vom 1. Januar eines jeden Jahres.

Tab.: 22 Das Wachstum der Forelle (*Salmo trutta*) im Torpatjärn.

Anzahl untersuchter Fische	Alter in Monaten	Mittelwert cm (Lt)	Variationsbreite cm
3	57	33,0	32,0—34,0
8	69	39,0	37,0—47,0

Tab.: 23 Das Wachstum der Forelle (*Salmo trutta*) im Rödingstjärn.

Anzahl untersuchter Fische	Alter in Monaten	Mittelwert cm (Lt)	Variationsbreite cm
8	18	17,3	14,5—19,0
20	30	21,1	18,0—22,5
11	42	26,0	24,0—27,5
9	54	30,3	28,0—33,0

Die Ergebnisse der verschiedenen Altersbestimmungen an der Forelle sind in Abb. 5 dargestellt. Das Überraschende dieser Untersuchung liegt in der Tatsache eines annähernd gleichen Wachstums der Forelle in völlig verschiedenen Lebensräumen. Auch zu dem vergleichsweise aufgetragenen Wachstum der Forelle aus dem Mitteldeutschen Bergland sind nur geringer Differenzen festzustellen.

Zum Wachstum der Forelle im Torpatjärn ist zu bemerken, dass alle Fische von 1947 und 1948 durchgeführten Implantierungen stammen. Der in einem Hochmoor gelegene abflusslose See war bis dahin nach Aussage des Gewässereigners ohne Fischbesiedlung.

Der ca. 3 ha grosse Rödingstjärn hat einen kleinen Auslauf zum Flusse Kvarnån. Neben einem fast ausschliesslichen Forellenbestand konnte im Sommer 1953 erstmalig ein Saibling (*Salmo fontinalis*) nachgewiesen werden. Der Fisch ist sicherlich vom Kvarnån aus aufgestiegen. Dort wurden 1952 einsömmerige Saiblinge ausgesetzt. Der Rödingstjärn wird stark mit Netzen befischt, künstlicher Brutbesatz erfolgt nicht. Nach Aufzeichnungen der Fischer wurden in einer Jahresperiode 1952/1953 ca 220 Fische gefangen. Bei einem Mittelgewicht von 200—250 g der gefangenen Fische, entspricht dies einem Hektarertrag von 15—20 kg im Jahr.

2.) Das Wachstum der Äsche (*Thymallus vulgaris*).

Dieser Untersuchung lagen die Altersbestimmungen an 67 Fischen aus den Flüssen Bodträskån, Spikselån und Kvarnån zu Grunde. Da ein verschiedenes Wachstum in den einzelnen Gewässern nicht vorlag, wurden wie bei der Forelle die Fliessgewässer geschlossen behandelt.

Tab.: 24 Das Wachstum der Äsche (*Thymallus vulgaris*) in den Fliessgewässern bei Bodträskfors.

Anzahl untersuchter Fische	Altersklasse	Mittelwert cm (Lt)	Variationsbreite cm
10	III	23,7	19,5—25,5
23	IV	29,2	24,0—32,0
17	V	34,1	31,0—37,5
8	VI	36,0	34,5—38,0
6	VII	37,7	36,5—39,5
3	VIII	39,5	38,0—41,0

Die hier gefundenen Wachstumswerte decken sich in allen Altersgruppen mit den Befunden von GUSTAVSON (1948) im Svartbäcken in Jämtland.

3.) Das Wachstum der Plötze (*Leuciscus rutilus*).

Wie in den Abbildungen 3 und 4 gezeigt werden konnte ist die Plötze in verschiedenen Seen des Untersuchungsgebietes der zahlenmässig dominierende Fisch. Bei der Vielzahl der aus allen Bereichen Europas vorliegenden Untersuchungen über diesen Fisch, war es von Interesse Wachstumsuntersuchungen an einer Population aus einem See des Waldgebietes durchzuführen. Es wurden 162 Fische aus dem vom Spikselån durchflossenen Tekakott-Träsk ausgewählt.

Tab.: 25 Das Wachstum der Plötze (*Leuciscus rutilus*) im Tekakott-Träsk.

Anzahl untersuchter Fische	Altersgruppe	Mittelwert cm (Lt)	Variationsbreite cm
16	VII	15,3	14,5—15,6
45	VIII	16,3	15,8—17,0
46	IX	17,7	16,8—19,5
42	X	19,0	17,8—20,0
13	XI	20,6	19,2—22,0

4.) Regional vergleichende Untersuchungen.

Eine klare Aussage über die Wachstumsleistung der Fische eines bestimmten Lebensraumes kann erst in regional vergleichenden Untersuchungen gegeben werden. In der Abb. 5 wurde in die Resultate der Untersuchungen an der Forelle aus dem nordschwedischen Bereich eine Vergleichswachstumskurve von Forellen aus dem Mitteldeutschen Bergland aufgezeichnet (Vergl. auch MÜLLER 1952). Die Differenz des Wachstums von *Salmo trutta* in den beiden sehr unterschiedlichen Bereichen ist nur gering, obwohl den Fischen des nordschwedischen Bereiches nur ein Bruchteil der Nahrungsmenge zur Verfügung steht. Da die Forelle in beiden Vergleichsbereichen intensiv genutzt wird, zeigt dieses Beispiel dass in beiden Bereichen die optimale Wachstumsleistung des Fisches in einem Bach- oder kleineren Flussbiotop gegeben ist. Dies ist unabhängig von der angebotenen Nahrungsmenge der Fall. Wie einleitend schon bemerkt wurde, kann man in der Regel eine Übervölkerung und eine damit verbundene Minderung der Wachstumsleistung nicht erwarten, da den Fischen in einem fliessenden Gewässer alle Ausweichmöglichkeiten gegeben sind. Das verminderte Nahrungsangebot wird sich deshalb nur in einer verminderten Bestandsdichte ausdrücken.

Für die Äsche (*Thymallus vulgaris*) liegen eine Reihe Vergleichsuntersuchungen aus den verschiedensten Bereichen vor, die in der folgender Tabelle gegenübergestellt sind.

Tab.: 26 Das Wachstum der Äsche (*Thymallus vulgaris*) in verschiedenen Wohngewässern.

Untersuchungsgewässer	Altersgruppe (Länge in cm) II	III	IV	V	VI	VII	VIII
Spikselån	—	23,7	29,2	34,1	36,0	37,7	39,5
Svartbäcken	15,9	23,2	28,5	31,7	33,7	37,8	—
Fulda	17,9	25,3	35,0	—	—	—	—
Alpenbäche	18,8	27,6	35,1	—	—	—	—

Die hier gegenübergestellten Wachstumswerte stimmen in den schwedischen Untersuchungen Spikselån und Svartbäcken (GUSTAVSON 1948) gut überein. Von der Altersgruppe IV an ist im Vergleich zu den Untersuchungen in der im Mitteldeutschen Bergland gelegenen Fulda und den Alpenbächen (SEEZ cit. MÜLLER 1952) aber eine merkbare Differenz festzustellen. Eine Erklärung kann aus den vorliegenden Untersuchungen hierfür nicht gegeben werden.

Das im Tekakott-Träsk beobachtete Wachstum der Plötze gehört zu den niedrigsten bisher beobachteten Wachstumswerten. Lediglich in einer Untersuchung ALMS (1917) im Yxtasjö konnten annähernd gleiche Werte beobachtet werden. Hier ist zweifellos eine zu hohe Bestandsdichte von *Leuciscus rutilus* anzunehmen. Die Ursache des Überhandnehmens dieser Fischart ist in der einseitigen Nutzung des Sees zu suchen. Eine intensive Befischung erfolgt nur auf *Esox lucius* — der einzige wesentliche Feind von *Leuciscus rutilus* wird systematisch dezimiert — eine solche Bewirtschaftungsweise muss zur Störung des Gleichgewichts führen, die sich in einer Massenbesiedlung von *Leuciscus rutilus* ausdrückt und aus der das geringe Wachstum resultiert. Im Nachfolgenden ist eine Übersicht des Plötzenwachstums in verschiedenen Skandinavischen Gewässern gegeben.

Tab.: 27 Das Wachstum der Plötze (*Leuciscus rutilus*) in verschiedenen skandinavischen Wohngewässern.

Gewässer	Altersgruppe (Länge in cm) VII	VIII	IX	X	XI
Ladogasee (JÄSKELAINEN)	20,4	22,8	26,7	29,6	—
Hjälmaren (ALM)	20,8	22,0	24,2	25,4	26,8
Yxtasjö (ALM)	—	14,9	17,2	18,5	—
Tekakott-Träsk	15,3	16,3	17,7	19,0	20,6

III. Untersuchungen zur Ernährung von *Salmo trutta* und *Thymallus vulgaris*

Wie in den vorliegenden Ausführungen schon verschiedentlich betont wurde, wurden in den Bächen und Flüssen des hier behandelten Unter-

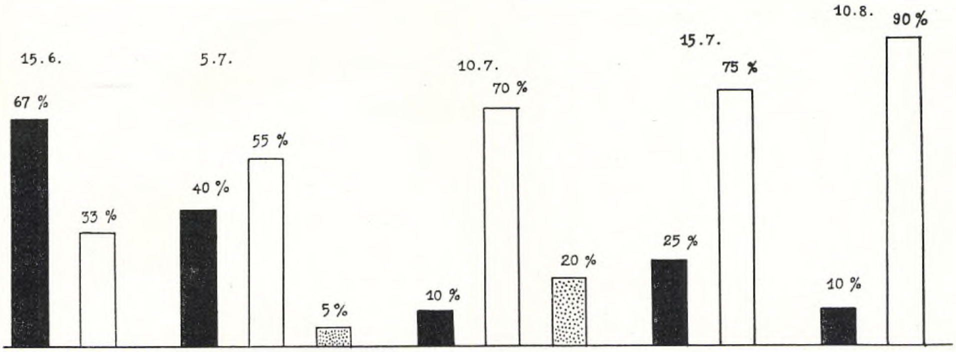

Abb.: 6 Die Nahrung der Forelle (*Salmo trutta*). Darstellung der Gewichtsprozente des Mageninhaltes. (Zeichenerklärung im Abb. 7.)

suchungsgebietes Regulierungen zum Zwecke einer rationelleren Flösserei durchgeführt. An anderer Stelle konnte gezeigt werden (MÜLLER 1953), dass sich die Zusammensetzung der Bodenfauna in den ersten beiden Jahren nach dem Eingriff qualitativ wesentlich verändert. Dabei ist bei grosser Individuenmenge ein einseitige Artzusammensetzung, mit einer Betonung rheophiler Insektenlarven, gegeben. Es war nun von Interesse zu verfolgen, in welchem Umfange sich die beiden Hauptfischarten *Salmo trutta* und *Thymallus vulgaris* diesem veränderten Nahrungsbild anpassen. Untersuchungen über die qualitative und quantitative Zusammensetzung der aufgenommen Nahrung wurden an Material aus dem Jahre 1952 und 1953 durchgeführt.

Es galt zunächst festzustellen in welchem Verhältnis die verschiedenen für die beiden Salmoniden möglichen Nahrungskomponenten sich während eines Sommerhalbjahres verteilen. In den Abb.: 6 und 7 sind diese Verhältnisse für die Forelle und die Äsche getrennt nach Bodennahrung, Fischnahrung und Luftnahrung aufgetragen. Nach einer anfänglich ungefähr mengenmässig gleichen Verteilung von Bodentier— und Luftnahrung, dominiert während der Sommerperiode die Luftnahrung. Die Fischnahrung spielt bei der Forelle nur eine untergeordnete Bedeutung und muss wohl als »Gelegenheitsnahrung» angenommen werden.

Für die 1953 an 52 Forellen und 56 Äschen durchgeführten Untersuchungen wurde eine mehr detailierte Darstellung der einzelnen Komponenten der Bodentiernahrung, gegenüber den anderen Nahrungsanteilen gegeben (vergl. auch Abb.: 8).

Dabei dominieren im Mai bei beiden Fischarten die *Simulium*-Larven als Nahrung. Diese Erscheinung ist verständlich. In diesem Monat und auch noch im Monat Juni liegt die Hauptentwicklungsperiode dieser Tiergruppe. Sie besiedelt in ausserordentlicher Menge die Geröllbiotope eines fliessenden Gewässers, in regulierten Abschnitten erreicht diese Larve die höchsten Besiedlungswerte. Dabei konnte *Simulium* nicht nur als stationäre, in der

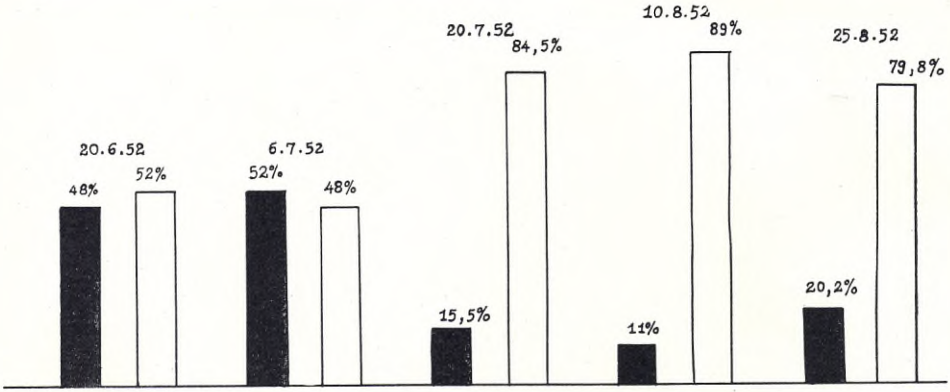

Abb.: 7 Die Nahrung der Äsche (*Thymallus vulgaris*). Darstellung der Gewichtsprozente des Mageninhaltes.

■ Bodenfauna.
▦ Fischnahrung.
☐ Luftnahrung.

Strömung lebende Larvenform, sondern auch in der Drift (Vergl. MÜLLER 1954 b) in grosser Anzahl nachgewiesen werden. *Simulium*-Larven konnten bei Fischen aller Altersklassen nachgewiesen werden. Es zeigte sich jedoch, dass bei jüngeren Forellen (Alterklasse I und II) in wesentlich höherem Prozentsatz als bei älteren zu beobachten waren. Bei *Thymallus vulgaris* konnte auch bei älteren Formen noch ein hoher Anteil an *Simulium* festgestellt werden (Äsche, 6.6.53,27 cm lang, Altersklasse IV — 312 *Simulium*-Larven als Mageninhalt). Das Schwergewicht der Nahrung bei der grösseren Forelle liegt demgegenüber eindeutig bei den Trichopterenlarven. *Hydropsychidae, Plectrocnemia* und *Neureclipsis,* seltener *Limnophilidae* waren die am häufigsten zu beobachteten Larvenformen. Dieser Nahrungsanteil tritt aber wesentlich erst im Monat Juni in Erscheinung. Interessant war bei den Untersuchungen des Sommers 1953, dass im Monat Mai von Forelle und Äsche *Limnea ovata* als Nahrung aufgenommen wurde. Fischnahrung wurde nur bei der Forelle beobachtet. Eine Forelle (32 cm, Altersgruppe V) wurde bei Hochwasser unterhalb eines Seeausflusses gefangen. Im Magen fanden sich 17 *Leuciscus rutilus.* (Längen 4—6 cm).

Im Monat Juni tritt eine starke Verschiebung des Nahrungsbildes bei der Forelle ein. Ephemeropteren, Plecopteren und Trichopteren sind die hauptsächlichen Nahrungsanteile. Bei der Äsche dominiert weiterhin die Larve von *Simulium.* Daneben ist ein auffallend grosser Anteil von *Limnea ovata* festzustellen. Eine Äsche von 25 cm hatte ausschliesslich *Limnea* aufgenommen (42), in anderen Fällen trat im Mageninhalt *Limnea* mit *Simulium*-Larven zusammen auf.

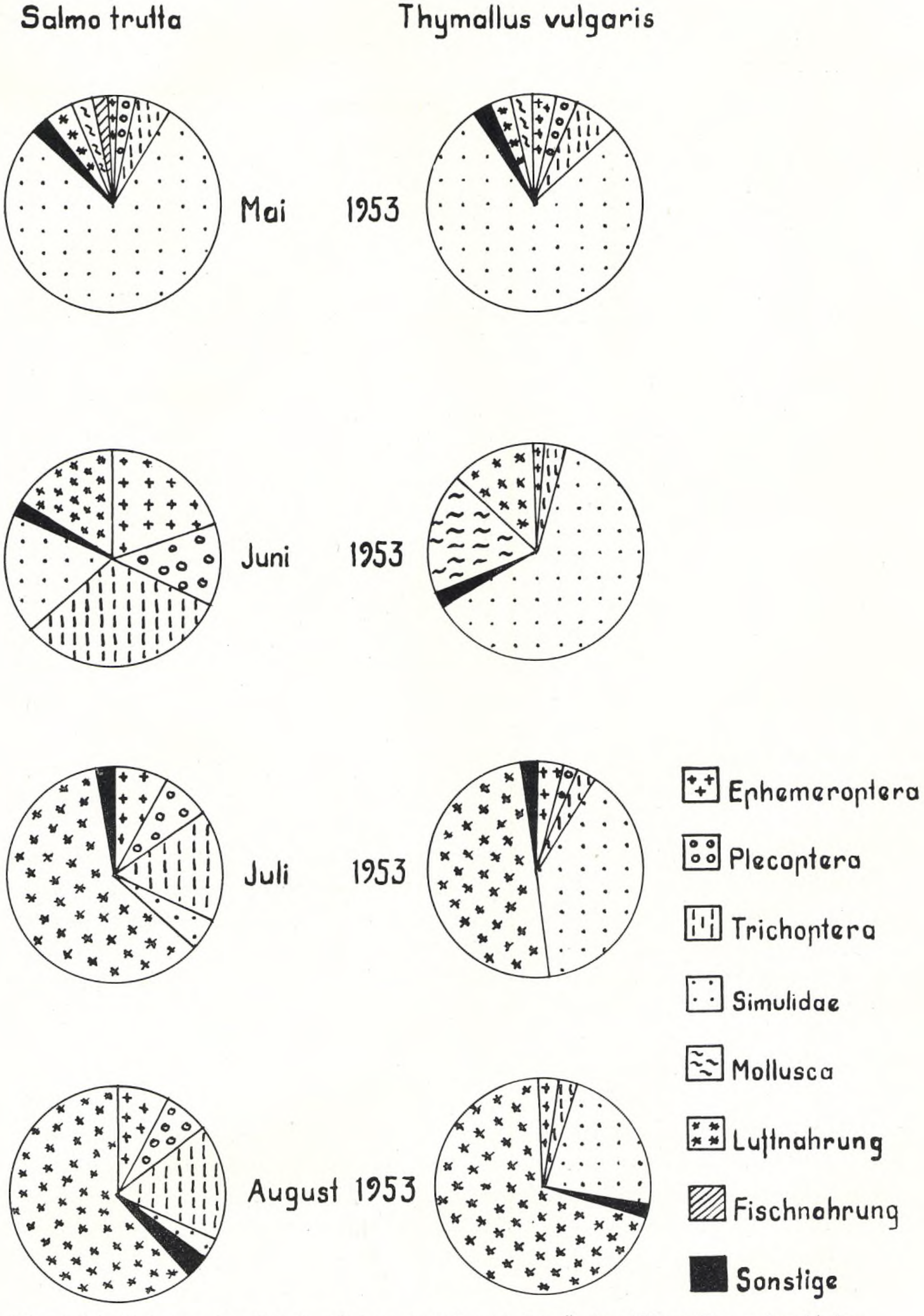

Abb.: 8 Die Nahrung der Forelle (*Salmo trutta*) und der Äsche (*Thymallus vulgaris*) im Sommer 1953.

In den Monaten Juli und August ist ein klares Dominieren der Luftnahrung zu erkennen. Neben den Imagines aquatischer Insekten sind fast alle Insektenformen des Waldgebietes anzutreffen. Besonders häufig sind Dipteren, Coleopteren und *Formicaria* zu beobachten.

Der Vergleich der Resultate von 1952 und 1953 zeigt prinzipiell eine gleiche Entwicklung.

Die 1953 im Monat Mai begonnen Untersuchungen zeigen einen fast ausschliesslichen Befund von Bodennahrung, der 1953 auch noch im Juni bestimmend ist. In den Beobachtungen des Jahres 1952 ist im Juni der Bodennahrunsanteil etwa bei beiden Fischen zu gleichen Teilen mit der Luftnahrung vertreten. Im Juli und August zeigen beide Beobachtungsjahre und bei beiden Fischarten die Befunde ein deutliches Überwiegen der Luftnahrung.

Eine solche Entwicklung ist aus den Fluktuationen denen die bentische Fauna während eines Sommerzyklus unterworfen ist, zu verstehen. Im dem hier behandelten Untersuchungsgebiet das ca 60 km unterhalb des Polarkreises liegt öffnet sich das Eis zwischen dem 1. und 15. Mai (1952 u. 1953, 1954). Die erste Eislegung erfolgte 1952 am 29. September, 1953 in der zweiten Hälfte Oktober (ungewöhnlich spät). Dies bedingt, dass Fauna und Flora eine nur kurze Entwicklungsperiode zur Verfügung steht. Im benthischen Lebensraum sind nach dem Aufgehen des Eises die höchsten Besiedlungswerte festzustellen. Diese Besiedlungswerte dauern in den Monaten Mai und Juni an. Bei den in Massen auftretenden Larven von *Simulium,* verschiedenen Chironomidengattungen, den Baetiden, *Ephemerellidae, Chitonophora, Rhyacophila, Hydropsychidae, Plectrocnemia, Neureclipsis* erfolgt bis zur Flugzeit in den Frühjarswochen ein starker Zuwachs, d.h. bis in die zweite Junihälfte ist in dem in Gewicht ausgedrückten quantitativen Bestand der Bodenfauna ein dauernder Anstieg zu konstatieren.

Man kann in diesem Ablauf ein natürliches Regulativ im Produktionskreislauf des Gewässers erkennen. Nach dem langen Winter in dem die meisten Bäche ausserordentlich starke Vereisungen zeigen ist der Nahrungsbedarf der Fische am grössten. Das hohe Angebot kann so von den Fischen optimal ausgenützt werden. Es hat nach unseren Beobachtungen den Anschein, als ob in dieser Periode der Hauptzuwachs der Salmoniden liegt. In der zweiten Junihälfte und im Juli erwärmen sich die kleinen Waldbäche ausserordentlich stark. Die Flugzeit der verschiedensten aquatischen Insekten setzt meist schlagartig ein. Anfang Juli sind die Gewässer weitgehend an allen Larvenformen verarmt. Hier setzt gleichzeitig der Übergang zur Luftnahrung ein. Die Nahrungsdiagramme der Jahre 1952 und 1953 zeigen deutlich den Eintritt der Flugzeit durch den Übergang zur Luftnahrung.

Nach der meist in der ersten Julihälfte erkennbaren Verarmung der Bodenregion an Insektenlarven, kann man schon Ende Juli und Anfang August steigende Werte erkennen. Die in der Hauptflugzeit von den verschiedenen Formen abgelegten Eier entwickeln sich sehr schnell, dies trifft besonders für die netzbauenden Trichopteren zu in den Bereichen in denen diese Larven die Drift der in Hochproduktion stehenden Seen ausnützen können.

Wie in der Nahrungsübersicht des Jahres 1953 zu ersehen ist wird von *Salmo trutta* auch die angebotene Ephemeropteren-, Plecopteren- und Trichopterennahrung in etwa gleichbleibendem Umfange ausgenützt.

Zur Frage des Einflusses der durch die Flössereiregulierungen bedingten Veränderung des qualitativen Nahrungsangebotes kann festgestellt werden:

1.) Das hohe (meist durch die Regulierungen bedingte) *Simulium*-Angebot wird besonders in den Monaten Mai und Juni von den Salmoniden maximal ausgenutzt. Auf Grund der Tatsache, dass das Auftreten dieser Larven in der Hauptfrassperiode am grössten ist, muss *Simulium* eine wesentliche produktionsbiologische Rolle zuerkannt werden.

2.) Es zeigt sich, dass im Verlaufe eines Sommerzyklus die Äsche (*Thymallus vulgaris*) in wesentlich grösserem Umfang *Simulium* als Nahrung aufnimmt als *Salmo trutta*. In dieser Hinsicht könnte man bei diesem Fisch von einer besseren Anpassung an die Bedingungen eines regulierten Gewässers sprechen.

Untersuchungen zur Nahrungswahl.

In den vorgehenden Ausführungen wurde eine mehr allgemeine Zusammenfassung der im Magen und Darmtraktus vorgefundenen Nahrungsteile dargestellt. Danach sind beide Fischarten zu den Konsumenten der Bodennahrung zu rechnen, im Hochsommer kommt hierzu ein wesentlicher Ergänzung in der Aufnahme einer überwiegenden Menge Luftnahrung. Diese Darstellungen entstammen nun einem grossen Material aus verschiedenen Teilen des Spikselån und des Kvarnån. Für einen Punkt aus dem Unterlauf des Flusses Spikselån wurde eine mehr detailierte Darstellung einer spezialisierten Auswahl beider Fische dargestellt. In der Abb.: 9 ist für den Punkt »Videselbro» ein Quersnitt der Bodenfauna während des Sommers 1952 dargestellt. An diesem Punkte (auf etwa 200 m Strecke) wurden in wöchentlichen Abständen Forellen und Äschen gefangen. Insgesamt liegen dieser Darstellung 12 Äschen und 10 Forellen zugrunde. Dargestellt wurde nur die aufgenommene Bodennahrung in den Monaten Juni und Juli 1952. Hierbei zeigt sich, dass beide Salmoniden deutlich zwei verschiedene Schwerpunkte in der Nahrungsaufnahme zeigen. Während *Thymallus vulgaris* die hohe Anzahl der Simuliiden annähernd in der gleichen Prozentzahl des Angebotes ausnutzt, liegt der Schwerpunkt der Nahrungsaufnahme der Forelle eindeutig bei den Trichopteren. Eine eingehendere Analyse der Befunde lässt eine Aussage über den Ort der Nahrungsaufnahme zu. Bei *Thymallus* (Vergl.: Abb.: 9) konnte neben den dominierenden Simuliiden auch eine relativ grosse Anzahl Trichopteren festgestellt werden. Hierbei handelte es sich fast ausschliesslich

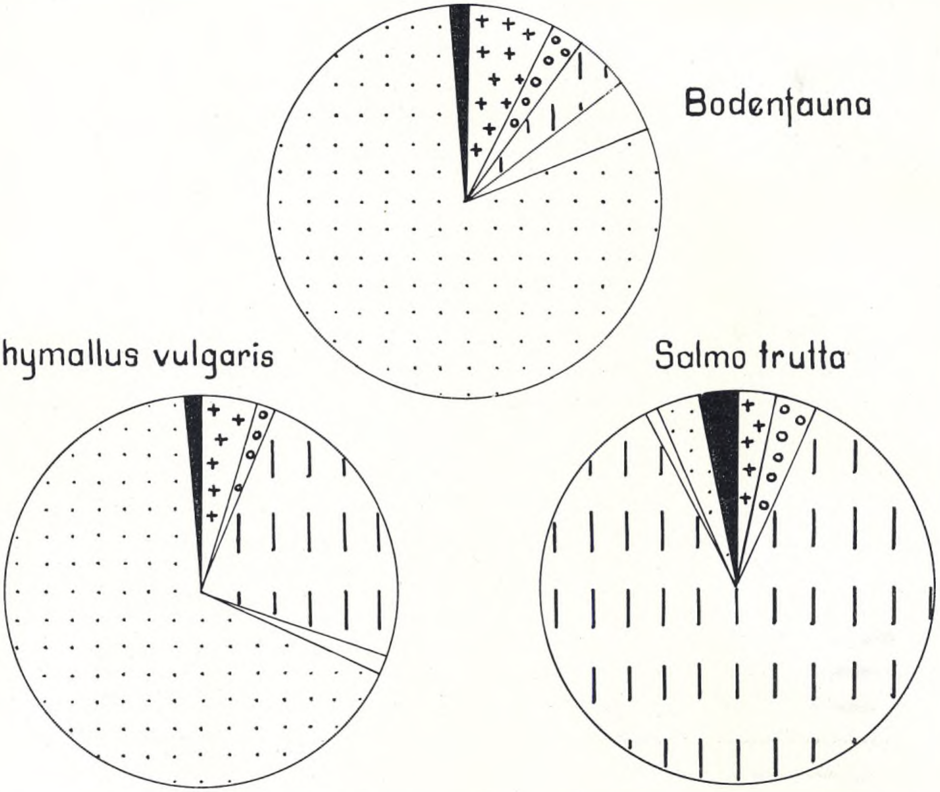

Abb.: 9 Die verschiedene Ausnützung der angebotenen Bodennahrung durch *Salmo trutta* und *Thymallus vulgaris*. (Zeichenerklärung in 10.)

um Larven der Gattung *Rhyacophila*. *Simulium* und *Rhyacophila* leben vergesellschaftet auf Steinoberflächen in starker Strömung. *Rhyacophila* deckt in grossem Umfange ihren Nahrungsbedarf aus *Simulium*-Larven. Mit dieser Larven zusammen wurde auch die Chironomide *Cardiocladius* als Mageninhalt angetroffen, von der bekannt ist dass sie von *Simulium*-Puppen lebt. Für *Thymallus* kann so der Ort der Nahrungsaufnahme sicher umgrenzt werden: strömungsexponierte Bereiche der Bachmitte mit aktiver Aufnahme der Nahrung von der Steinoberfläche.

Die bei der Forelle angetroffenen Thichopteren gehörten fast ausschliesslich den Gattungen *Hydropsyche* und *Limnophilus* an, dabei waren die *Hydropsychidae* vorherrschend. Die hier beobachteten Limnophiliden lebten meist in ruhiger Bereichen hinter grösseren Steinen und auch in der Uferregion. Die *Hydropsychidae* in stark turbulenter Strömung, wo diesen fangnetzbauenden Larven die besten Ernährungsmöglichkeiten gegeben sind. So lässt sich auch der Ort der Nahrungsaufnahme der Forelle relativ klar definieren: Bereiche verminderter Strömung und an solchen Punkten meist,

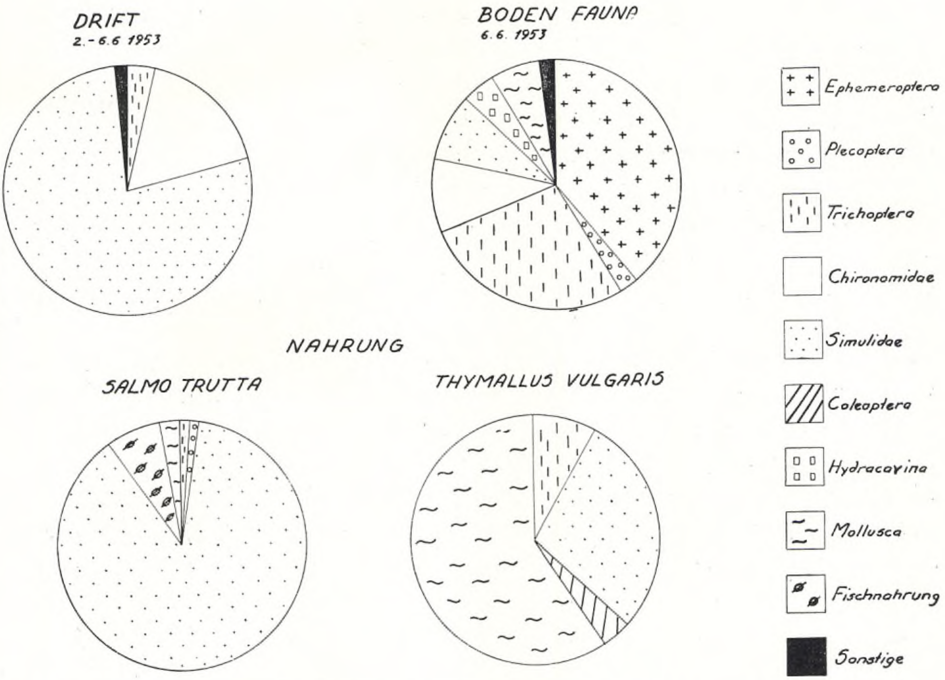

Abb.: 10 Die Ausnützung von Drift und Bodenfauna als Nahrung von *Salmo trutta* und *Thymallus vulgaris*. Nach Beobachtungen im Unterlauf des Flusses Kvarnån bei »Kvarnhultskoja».

wo turbulenten Zonen anzutreffen sind. Ein aus den Nahrungsbefunden ableitbarer Aufenthalt in der Uferregion erscheint unwahrscheinlich.

Diese Analyse des Nahrungsbildes vermittelt für diese beiden Fischarten zwei deutlich physiographisch und ökologisch verschiedene Räume (Nischen). Beiden Formen ist so eine optimale Ausnützung ihrer Nische gegeben.

Die Darstellung ist insofern unvollkommen, weil sie die mögliche Konkurrenz anderer Arten nicht behandelt. In der Durchführung befindliche Untersuchungen zeigen, dass besonders der Forelle durch das Auftreten von *Cottus gobio* eine starke Nahrungskonkurrenz erwächst. An anderer Stelle war vom Autor (MÜLLER 1952) schon mit einem umfangreicheren Material aus Mitteleuropa auf die Tatsache hingewiesen worden.

Ein solcher wie hier gezeigter Befund kann bei dem qualitativ und quantitativ starken Schwankungen unterliegenden Nahrungsangebot eines Fliessgewässer selbstverständlich nie in ein starres System eingefügt werden. So zeigte sich in einer anderen Untersuchung für *Thymallus* ein prinzipiell gleiches Bild wie es hier aufgezeigt wurde, während die Forelle ihren Nahrungsbedarf aus einer anderen Nahrungskomponente deckte. In Abb.: 10

ist eine Untersuchung vom Juni 1953 aus dem Flusse Kvarnån dargestellt. Die Beobachtungen wurden im Zusammenhang mit der Erscheinung getroffen, dass in einem fliessenden Gewässer neben einer stationären Fauna eine dauernde Drift lebenden und toten organischen Materials erfolgt. (Vergl. auch MÜLLER 1954 b).

Für einen Punkt des Unterlaufes des Flusses wurden der Bestand der Bodenfauna auf einer grösseren Fläche ermittelt und gleichzeitig Untersuchungen über die am gleichen Orte vorliegende Drift durchgeführt. In beiden Nahrungsbildern dominieren die Simuliiden. Auffallend ist der Anteil der bei *Thymallus* angetroffenen Molluscen (*Limnea ovata*). *Limnea* besiedelt wie *Simulium* die Steinoberflächen. Da die Untersuchungen zur Zeit des Frühjahrshochwasser gemacht wurden, lagen in den von *Limnea* besiedleten ruhigeren Uferbereichen wesentlich höhere Strömungswerte als bei Normalwasserstand vor. In der Art der Nahrungsaufnahme kann für *Thymallus* ein gleiches Verhalten wie in der vom Spikselån gezeigten Untersuchung angenommen werden, dass also der Fisch seine Nahrung aus den strömungexponierten Steinoberflächen entnimmt. Für *Salmo trutta* kann aus den Beobachtungen im Spikselån (Abb.: 9) ebenfalls ein gleiches Verhalten wie dort angenommen werden. In den w.o. definierten Aufenthaltsort der Forelle, in ruhigeren Bereichen unterhalb turbulenter Strömung liegt erfahrunsgemäss das höchste Angebot treibender Nahrungstiere und -partikel vor. Es ist verständlich dass der Fisch dieses hohe Angebot hier voll ausnützt — ohne »seine» Nische zu verlassen.

Beide Untersuchungen zeigen demnach eine relativ klare Abgrenzung der Orte der Nahrungsaufnahme zweier Fischarten. Sie geben weiterhin eine Antwort auf die Feststellung, dass trotzt einer qualitativ starken Übereinstimmung des Nahrungsbildes (*Simulium*) die dominierende Komponente in völlig verschiedenen Räumen aufgenommen ist — eine Konkurrenz also nicht vorliegt.

IV. Die Fischereiwirtschaftliche Bedeutung der untersuchten Gewässer

Wie in den Untersuchungen über die Bodenfauna des hier behandelten Gebietes mitgeteilt wurde (MÜLLER 1953) sind alle Fliessgewässer in die Gruppe der »Nahrungsarmen» einzustefen. Die »*Capacité biogénique*» erreichte nur unter den günstigsten Bedingungen den Grad III (l.c. p. 121).

Das geringe natürliche Nahrungsangebot lässt erwarten, dass die Erträge der Gewässer entsprechend niedrig liegen. Hinzu kommt, dass reine Salmonidengewässer in den Bächen nur selten angetroffen werden. Wie an anderer Stelle ausgeführt wurde sind die Fliessgewässer in ihrer Gesamtheit dem Unterlauf einer zentraleuropäischen Salmonidenregion gleichzusetzen (MÜLLER 1954 a).

Diese Tatsache bedingt das Eindringen vieler eurythermen Formen, wobei vorallem das Auftreten von *Esox lucius* und das unterhalb von Seen beobachtete Eindringen von *Perca fluviatilis* als für alle Salmoniden nachträglich angesehen werden muss. Als wertvollste Gewässer müssen die kleineren Waldbäche angesehen werden, die wie hier an den Beispielen Skravelbäcken und Mörtträckbäcken zahlenmässige Salmonidenanteile von über 60 % des Gesamtbestandes aufweisen. Diese Bedingungen sind aber nur in Bereichen starker Strömung gegeben. Bekanntlich wechseln aber laufend lotische und lenitische Bereiche einander ab, oft sind in diesen Verlauf grössere oder kleinere Seen eingeschaltet, die Voraussetzungen für das Eindringen von Konkurrenten bzw. Feinden für den Salmonidenbestand sind also an vielen Punkten des Gewässers gegeben. Dies muss in hohem Umfange als wertmindernd bei der Beurteilung der Gewässer betrachtet werden.

Neben der Gewinnung eines qualitativen Überblickes über den Fischbestand geben die quantitativen Abfischungen mit dem Elektrogerät gleichzeitig einen wertvollen Aufschluss über die Gewichtsverteilung der einzelnen Arten und den Anteil der nutzbaren Fische. Es wurden für diese Untersuchung drei typische Beispiele ausgewählt.

Im Mörtträskbäcken ist ein kleiner Waldbach von ca 3 km Länge gegeben. Der Bach kommt aus einem kleinen in einem Sumpfgebiet liegenden See (Tjärn) und fliesst mit einer mittleren Strömungsgeschwindigkeit von 0,60—0,80 m/sec zum Bodträskån. In seinen Verlauf sind nur kleinere Abschnitte geringerer Strömung eingeschaltet. Wie die Abfischungsresultate zeigen ist hier ein reiner Forellenbach gegeben in dem neben der Forelle, nur die typischen Forellenbegleiter *Phoxinus* und *Lota* auftreten. Die in dem Quellsee vorkommenden *Leuciscus rutilus* und *Esox lucius* konnten im Bachlauf selbst nicht beobachtet werden. Die geringe Grösse des Baches setzt hier dem Auftreten dieser Fische eine Grenze.

Der Skravelbäcken war schon an anderer Stelle eingehender geschildert worden. Für die hier zu behandelnden Überlegungen wurde ein Bereich des Unterlaufes ausgewählt.

Die nächst höhere Grössenordnung eines Fliessgewässers ist in dem Spikselån gegeben. Hier wurde ein typischer, unregulierter Bereich des Mittellaufes ausgewählt.

Für eine fischereiwirtschaftliche Beurteilung der hier zu behandelnden Gewässer ist neben der qualitativen, zahlenmässigen Verteilung der einzelnen Arten, das Gewicht der Fische und besonders das der vorgefundenen Salmoniden von ausschlaggebender Bedeutung.

Im Nachfolgenden sollen die Untersuchungen 4 (Tab.: 4) des Skravelbäckens, Untersuchung 4 (Tab: 12) des Spikselån und die Untersuchung des Mörtträskbäckens (Tab.: 20) vergleichend behandelt werden.

Tab.: 28 Übersicht über Anzahl und Gewicht der gefangenen Fische in den Vergleichsgewässern.

Untersuchungsort	Abgefischte Wasserfläche (m^2)	Zahl der Fische m^2	Gewicht der Fische g/m^2
Mörträskbäcken	120	0,13	12,5
Skravelbäcken (4)	100	0,11	8,4
Spikselån (4)	405	0,21	7,1

Diese Gegenüberstellung zeigt, dass der kleinste Bach den höchsten Gewichtswert pro Flächeneinheit aufweist. Noch deutlicher wird die fischereiwirtschaftliche Überlegenheit dieses Gewässertypus, wenn wir die Gewichtsanteile der Salmoniden in den drei Untersuchungen gegenüberstellen.

Tab.: 29 Der Anteil der Salmoniden am Gesamtfischbestand.

Untersuchungsort	Gesamtfischgewicht g/m^2	Salmonidengewicht g/m^2
Mörtträskbäcken	12,5	9,5
Skravelbäcken (4)	8,4	8,2
Spikselån (4)	7,1	2,6

Die in den drei verschiedenen Bachtypen angetroffenen Befunde entsprechen also einem ha-Bestand der Salmoniden von 95,82 und 26 kg. Nach den Untersuchungen von AMMAN (1952) und nach eigenen Beobachtungen (MÜLLER 1954 c) zeigt sich in einem natürlichen Gewässer, dass man von dem Gesamt-Salmonidenbestand ca 20—25 % zu den nutzbaren Fischen rechnen kann. Daraus lässt sich angenähert der zur Zeit der Untersuchung angetroffene Nutzwert des Wassers berechnen. Mit 5—8 kg liegt er im Spikselån am niedrigsten. Skravelbäcken und Mörtträskbäcken weisen ungefähr gleiche oder doch sehr ähnliche Verhältnisse mit 16—24 kg auf.

Für die beiden letztgenannten Bäche kommen die hier aufgezeigten Resultate zu dem annähernd gleichen Ergebnis der Produktivität des Gewässer, wie wir sie aus den Untersuchungen über die Quantität der Bodenfauna erwarten mussten (Vergl. MÜLLER 1953 p. 90 ff.). Der stark gemischte Fischbestand und der damit verbundene Nachteil für die Entwicklung der Salmoniden führt zu einer deutlichen Ertragsminderung. Eine nur auf eine »Bonitierung» aufbauende Untersuchung würde hier zu missweisenden Resultaten führen.

V. Die wirtschaftliche Nutzung der untersuchten Gewässer

Eine bodenständige Berufsfischerei fehlt in dem hier behandelten Gebiet heute gänzlich. Mit der verkehrstechnischen Erschliessung des Gebietes und der Verlagerung der Erwerbsquellen zur Holzwirtschaft hat die Fischerei wesentlich an Bedeutung verloren. Spuren einer bodenständigen Fischerei zeigen sich lediglich noch in der Lappensiedlung Rödingsträsk, in der die Fischerei noch als notwendiger Nebenerwerb angesehen werden kann.

Diese Entwicklung muss als eine der wesentlichen Ursachen der qualitativen Verschlechterung aller Gewässer, besonders der Seen angesehen werden. Eine systematische Befischung erfolgt nur während der Laichzeit des Hechtes in den Strandzonen der Seen mit Reusen und eine intensive Sportfischerei in allen fliessenden Gewässern auf Salmoniden. Umfang, Intensität und Art dieser Fischerei müssen als einseitiger Raubbau angesprochen werden. Hier sind die Gründe zu suchen die zu der oft zu beobachtenden Störung des Gleichgewichtes der Arten untereinander führen und die letztlich die Massenentwicklung wertloser Fische zur Folge hat.

In oft falscher Einschätzung der tatsächlichen Gegebenheiten versucht man durch Verbotstafeln und oft unkontrollierte Implantierungen die fischereilichen Verhältnisse zu bessern. Beide Massnahmen können nicht zu einer Verbesserung führen. Den oft mit grossem staatlichen und privaten Geldeinsatz durchgeführten Implantierungen in bereits besiedelten Seen waren fast durchweg ein Misserfolg beschieden. Lediglich in fischfreien Seen (Vergl. Beispiel Torpatjärn) und in Seen mit reinem Salmonidenbestand (Vergl. Beispiel Rödingstjärn) konnten gute Resultate erzielt werden. Die seit Jahren durchgeführten Implantierungen in den fliessenden Gewässern sind weitgehend unkontrollierbar in ihren Auswirkungen und rechtfertigen m.E. nicht eine Fortführung in der bisherigen Weise.

Nehmen wir die derzeitige Lage der fischereilichen Nutzungsmöglichkeit der Gewässer des Bodträskforsbereiches als Ausgangspunkt, so ergeben sich auf Grund unserer Beobachtungen und Untersuchungen folgende Wege und Möglichkeiten einer Verbesserung des Nutzungswertes.

Um die fliessenden Gewässer in ihrer Gesamtheit in Richtung eines höheren Salmonidenertrages zu verbessern, halte ich einen intensiven Einsatz des Elektrofischgerätes für unbedingt erforderlich. Nur so kann eine gründliche Kontrolle des Fischebestandes und eine Beseitigung der nicht erwünschten Fische erfolgen. Besonders in Gewässern von der Grössenordnung des Spikselån würde sich eine Bestandsregulierung mit Hilfe des Elektrogerätes sicher zu Gunsten eines gesteigerten Salmonidenertrages auswirken.

Die Verbesserungsmöglichkeiten in den Seen gestalten sich schwieriger. Sie können nur durch eine sehr intensive Fischerei d.h. durch eine Bestandsverminderung erreicht werden. Mit den derzeitigen Methoden würde sich die Ausfischung zu kostspielig gestalten. Der Arbeitsaufwand würde in keinem Falle in einem Verhältnis zu der später erreichbaren Verbesserung stehen. Hier kann nur eine Entwicklung der Elektrofischerei in Seen zu einem Resultat führen. Weiterhin zeigt sich aber in verschiedenen Versuchen die Möglichkeit z.B. in mit *Perca fluviatilis* übervölkerten Seen durch Implantierung grösserer Coregonen, die die massenhaft vorhandene Percabrut als Nahrung ausnutzen können, die Barschentwicklung zu bremsen und durch die Coregonen den fischereilichen Wert des Wassers zu steigern.

Zusammenfassung

In den vorliegenden Ausführungen wurde ein Überblick über Vorkommen, Verbreitung und Bestandsdichte der Fische im Bereich des Flussystems des Bodträskån durchgeführt. Die in den Jahren 1952—1954 durchgeführten Untersuchungen zeigen, dass eine deutliche regionale Zonierung in den Gewässern nicht vorliegt. Lediglich in den kleinsten Fliessgewässern in denen dem Auftreten eurythermer Fische eine Grenze gesetzt ist — ist eine reiner Salmonidenbestand mit den typischen Begleitformen *Cottus, Phoxinus* und *Lota* gegeben.

Vorherrschend sind Fliessgewässer in denen neben den Salmoniden *Salmo trutta* und *Thymallus vulgaris* eurytherme Formen — *Esox lucius* und *Perca fluviatilis* auftreten.

In den meist mit *Leuciscus rutilus* und *Perca fluviatilis* übervölkerten Seen treten die kaltstenothermen Salmoniden deutlich zurück.

Regional ist nach unseren Untersuchungen die Fischfauna des gesamten Untersuchungsgebietes dem Unterlauf einer zentraleuropäischen Salmonidenregion gleichzusetzen.

Die Wachstumsuntersuchungen zeigten für die Forelle (*Salmo trutta*) ein nur wenig differierendes Wachstum in drei physiographisch sehr verschieden gestalteten Lebensräumen. Auch der Vergleich des Wachstums von *Salmo trutta* einer zentraleuropäischen Population zeigt nur geringe Unterschiede.

Das Wachstum von *Thymallus vulgaris* ist mit dem von GUSTAVSON in Jämtland festgestellten, nahezu identisch.

Für *Leuciscus rutilus* wurde an Material aus einem typischen Waldsee des Untersuchungsgebietes das Wachstum bestimmt. Als Folge der Übervölkerung des Sees konnte eine ausserordentlich geringe Wachstumsintensität konstatiert werden.

Die an *Salmo trutta* und *Thymallus vulgaris* durchgeführten Nahrungsuntersuchungen zeigen für beide Fische in den Frühsommermonaten ein Vorherrschen der Bodentiernahrung. Im Hochsommer dominiert in beiden Fällen die Luftnahrung.

In der Nahrungswahl beider Fische konnten auf Grund der Analyse des Mageninhaltes eine Aussage über den Aufenthaltsort gemacht werden. Es zeigte sich, dass beide Arten in verschieden gestalteten Räumen (Nischen) der Gewässer ihre Nahrung aufnehmen — eine Konkurrenz in der Auswahl der Bodennahrung demnach zwischen beiden Arten also nicht besteht.

In Untersuchungen über den fischereiwirtschaftlichen Wert, zeigte sich an

drei typischen Bachbereichen ein Hektarbestand von 95, 82 resp. 26 kg Salmoniden (*Salmo trutta* und *Thymallus vulgaris*). 20—25 % dieses Bestandes können als verwertbarer Bestand angesehen werden.

Zur Nutzung der Gewässer wurden auf Grund unserer Untersuchungen Vorschläge zu einer Verbesserung des Bestandes und des Nutzungswertes der fliessenden Gewässer und See unterbreitet.

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Über die Einwirkung des Grubenwassers auf die Kieselalgenflora in einigen oligotrophen Seen in Västerbotten

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Die vorliegende Untersuchung gehört zu einer Reihe allgemeiner biologischer Untersuchungen des sog. Gillervatten (Giller-Wasser) wegs, der mehrere grössere und kleinere Seen in der Nähe des Grubenortes Boliden im Västerbotten-Bezirk (Län) umfasst. (Siehe Karte Fig. 1.) Sie wurde veranlasst durch ein von Norrbygdens Wassergericht im April 1949 bewilligtes Gesuch der Grubenverwaltung Boliden, Abwasser der Grube und eines in Boliden geplanten Anreicherungswerkes abzuleiten, und zwar in erster Linie in den in der Nähe des Ortes belegenen Höbäckstjärn. Dieser kleine See steht durch einen Auslaufbach, den Höbäcken, in Verbindung mit dem See Gillervattnet, der früher in westlicher Richtung durch den See Bjurträsket und den Bach Kvarnbäcken, der sich in den Skellefte-Älv ergiesst, entwässert wurde.

Durch Entscheidung von 1949 hat die Gesellschaft das Recht erhalten zum Schutze der bebauten Strände des Bjurträsket, einen neuen Abwasserweg vom Gillervattnet in südlicher Richtung zu öffnen. Dieser Weg besteht aus einem neu gezogenen, 1,2 km langen Graben, der das Wasser von dem abgedämmten Gillervattenbach nach dem Brubäcken und von dort durch den Bruträsket zum Skellefte-Älv leitet. Die Gesellschaft erhielt auch die Genehmigung, den Höbäckstjärn, den Höbäcken, das Gillervattnet und gewisse Bezirke unterhalb des Auslaufs des Gillervattnet als Schlamm- und Klärungsteiche für das Abwasser anzuwenden. Für dessen Ableitung waren 3 Etappen vorgesehen: Während der ersten Etappe, in der das geplante Anreicherungswerk aufgebaut wurde, sollte nur das Grubenwasser der Bolidengrube — d.h. das Wasser, das in die Grubengänge eindringt — abgeleitet werden. Nach Errichtung des Anreicherungswerkes sollte auch dessen Wasser abgeleitet werden und diese 2. Ableitungsetappe sollte so lange dauern, als die Bolidengrube in Betrieb bleiben würde, nämlich etwa 10 Jahre. Danach sollte in der letzten Etappe nur noch Anreicherungswasser abgelassen werden. Die Entscheidung gewann am 6.6.1950 Rechtskraft. Später, im Juni 1952, erhielt die Grubengesellschaft weiter die Genehmigung, häusliches Abwasser des Ortes Boliden in den Höbäckstjärn abzulassen. Der neue

Wasserweg wurde im Juni 1951 für das Grubenwasser in Gebrauch genommen. Das Abwasser des in dem auf die Entscheidung folgenden Jahre gebauten Anreicherungswerkes wurde von August 1953 an abgelassen.

Die Beschaffenheit des Abwassers

Der Erzgang der Bolidengrube, der ältesten der Gruben, die der Gesellschaft in diesem Gebiet gehören, findet sich im Urgestein, und besteht aus verschiedenen Metallerzen, hauptsächlich Eisen und Zink mit Einschlag von Kupfer, Arsenik und Blei. Auch erhebliche Mengen Schwefel, wahrscheinlich in der Form von Schwefelkies (FeS_2) kommen vor. Das Grubenwasser, das auf seinem Weg durch das Gestein Bestandteile von Erzstaub und Verwitterungen aufnimmt, wird in Bassins auf verschiedenem Niveau in der Grube gesammelt, von wo es in den Vorfluter gepumpt wird. Die Beschaffenheit des Grubenwassers wird von verschiedenen Faktoren, wie denen der Zusammensetzung des Erzes und des Umfanges der Oxidation beeinflusst. Wenn in einem Erzlager mit Einschlag von Schwefelkies Luft Zutritt hat, kommt oft eine Oxidation zu Schwefeldioxyd vor, das sich im Wasser in Schwefelsäure auflöst, wobei das Grubenwasser freie Sulfatjonen und einen sauren Charakter bekommt. Weiter enthält das Grubenwasser verschiedene Metallsalze, deren Menge von Zeit zu Zeit wechseln kann, deren Zusammensetzung aber im Grossen gesehen konstant ist. Die Zusammensetzung des Grubenwassers ergibt sich aus Tab. 1, die einige Jahresdurchschnittswerte des Grubenwassers auf einem Niveau von 130 m Tiefe zeigt.

Das Wasser des Anreicherungswerkes enthält grosse Mengen unorganischen Schlammes, aber nur in geringem Umfange aufgelöste Verunreinigungen. Bei dem Anreicherungsprozess werden in weitem Masse solche Zusatzstoffe angewandt, die dem Wasser eine fast alkalische Reaktion mit pH-Werten verleihen, die um 7 liegen oder 7 übersteigen.

Das häusliche Abwasser schliesslich erfährt vor seinem Ablassen keinerlei Reinigung, aber seine schädliche Einwirkung auf den Vorfluter dürfte wesentlich dadurch herabgesetzt werden, dass in dem Höbäckstjärn eine sehr wirkungsvolle Schlammausscheidung durch Mischung mit dem giftigen Grubenwasser und auch eine bakteriologische Reinigung geschieht.

Tabelle 1. Analysen des Grubenwassers von Boliden, 130 m Tiefe. Jahresdurchsnittswerte.

Jahr	pH	SO_4 mg/l	Cu mg/l	Fe mg/l	Zn mg/l	As mg/l	Mn mg/l
1950	3,0	1.866	21	282	47	16	9
1951	2,9	1.400	15	195	32	9	4
1952	4,0	2.181	19	255	37	9	4

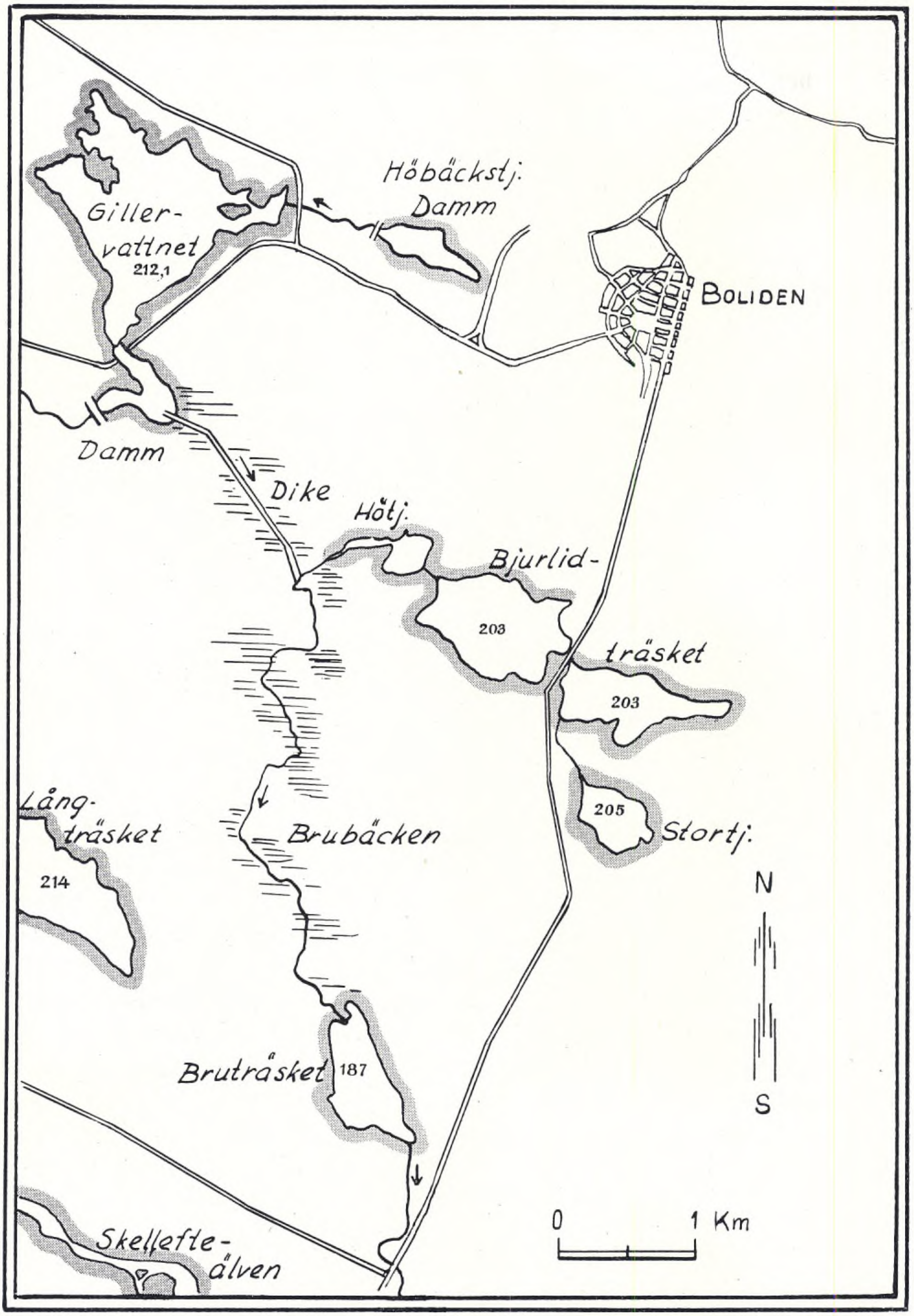

Fig. 1. Karte über die untersuchten Seen. Die Ziffer bezeichnen Höhe ü. M. »Dike» bezeichnet der neugezogene Graben zwischen dem Gillervattnet und dem Brubäcken.

Probeentnahme- und Untersuchungsmethodik

Wie bereits erwähnt, hat sich unsere Untersuchung im wesentlichen auf die biologischen Verhältnisse beschränkt. Nach früheren, mehr sporadischen chemischen Untersuchungen gewisser Punkte des Wasserwegs wurden diese ab 1951 regelmässig, und zwar zunächst durch das Zentrallaboratorium der Grubengesellschaft in Rönnskär und später durch das Staatliche Institut für Volksgesundheit, ausgeführt. Die Ergebnisse von vier dieser chemischen Untersuchungen, die gleichzeitig oder möglichst gleichzeitig mit den biologischen Probeentnahmen vorgenommen wurden, ergibt sich aus Tab. 2 a, 2 b, 4 und 6. Die biologischen Proben wurden bei drei verschiedenen Gelegenheiten entnommen und umfassen Proben sowohl für eine allgemeine biologische Untersuchung, als auch für die untenstehende spezielle Kieselalgen-Analyse des Höbäckstjärn-Höbäcksån, des Gillervattnet und des Bruträsket. Die erste und zugleich umfassendste Probeentnahme geschah am 29/30 August 1950, bevor der neue Wasserweg für die Ableitung des Grubenwassers geöffnet wurde. Sie wurde durchgeführt, um einen Begriff von der Flora und Fauna der Seen unter normalen Verhältnissen und damit eine Ausgangslage für die weiteren Studien nach dem Ablassen des Grubenwassers zu erhalten. Die nächste Probe wurde in der Zeit vom 18.—20. August 1952 entnommen, nachdem die Seen während eines Jahres Grubenwasser aufgenommen hatten. Aus dem Jahre 1953 liegt eine Probe vom 8. August vor, die bezüglich der Kieselalgen jedoch nicht so eingehend wie zuvor untersucht wurde.

Die biologischen Probeentnahmen geschahen teils mit Planktonnetz vom Strand und in grösseren Seen vom freien Wasser aus, teils mit Pfahlkratzer in der Strandvegetation und auf Steinen des Bodens. Zum näheren Studium der Kieselalgen wurde weiter eine Anzahl Proben aus dem Oberflächenbodenschlamm in den Seen entnommen. Diese Proben wurden dann nach der gewöhnlichen Methode mit konz. Schwefelsäure (modifizierte Methode nach H. RAABE) und mit Sirax als Einbettungsmittel behandelt. Die relative Häufigkeit der verschiedenen Arten ist in den Tabellen mit folgenden Zeichen angegeben:

ccc = Massenvorkommen
cc = sehr häufig
c = häufig
++ = ziemlich häufig
+ = nicht selten
r = selten
rr = vereinzeltes Vorkommen

Der Höbäckstjärn und der Höbäcken

Der erste der betroffenen Seen, der kleine Höbäckstjärn, hat eine grösste Länge von ca. 500 m und eine grösste Breite von 200 m. Der Boden dieses wie der übrigen Seen besteht aus Urgestein. Der Höbäckstjärn wird durch den Höbäcken entwässert, der sich etwa 800 m unterhalb des Auslaufs in den See Gillervattnet ergiesst. Die Umgebung des Sees und des Ablaufbachs besteht grösstenteils aus Sumpfböden und ist ganz unbewohnt.

Die Proben für die chemischen Analysen im Höbäckstjärn im Jahre 1950 sind am östlichen Strand, und im Höbäcken kurz vor dessen Einlauf in das Gillervattnet genommen. Das Resultat der chemischen Untersuchungen geht aus Tab. 2 a und b hervor. Die pH-Werte betragen 7,1—7,4, die Alkalinität$=$ 0,20—0,45. $SO_4=10$ im Höbäcken, $Fe=0{,}30$ und $Mn=<0{,}1$, während alle übrigen Metalljonen im Höbäcken nur spärlich vorkommen. Die gefundenen Werte sind für einen See im Urgesteinsgebiet als normal zu bezeichnen. Der relativ hohe pH-Wert deutet darauf hin, dass das Wasser des Sees trotz des umgebenden Moorbodens von Humus nicht erkennbar beeinflusst ist.

Tabelle 2 a. Höbäckstjärn. Chemische Analyse.

Datum	pH	Alkal. ln. HCl/l	SO_4 mg/l	Mn mg/l	Cu mg/l	Pb mg/l	As mg/l	Zn mg/l
29.8.—50	7,1	0,20	—	—	—	—	—	—
26.9.—50	—	—	—	—	—	—	—	—

Tabelle 2 b. Höbäcken. Chemische Analyse.

Datum	Trübung ^{0}ZPlO^5	pH	Alkal. ln. HCl/l	SO_4 mg/l	Fe mg/l	Mn mg/l	Cu mg/l	Pb mg/l	As mg/l	Zn mg/l
29.8.—50	—	7,4	0,45	10	0,30	$<0{,}1$	$<0{,}05$	$<0{,}05$	$<0{,}05$	$<0{,}05$
26.9.—50	—	—	—	—	—	—	—	—	—	—
19.8.—52	135	3,2	0	1.150	29,0	9,5	8,0	1,9	$<0{,}05$	40,0
8.8.—53	200	2,8	0	1.023	27,6	4,4	6,0	3,0	0.04	27,0
17.3.—54	645	6,9	0,65	530	1,3	0,7	0,05	$<0{,}05$	$<0{,}05$	1,5

Die biologischen Proben des Jahres 1950 wurden im Höbäckstjärn sowohl vom östlichen als auch vom westlichen Strand aus mit Planktonnetz und Pfahlkratzer genommen und am Orte selbst mit Formalin fixiert. Das Resultat der direkten Untersuchung ergibt sich aus Tab. 3. Ein Teil der Planktonprobe wurde zum näheren Studium der Kieselalgen mit H_2SO_4 behandelt. Die Arten ergeben sich aus Tab. 8. Dem Kieselalgenbestand des Höbäckstjärn fehlen, wie man ja in diesem seichten See nicht anders erwarten kann, echte Planktonformen. Die gefundenen Arten gehören alle zum Benthos und sind als solche typisch für einen kleinen, oligotrophen See. 103 Arten und Varieteten wurden verzeichnet, die Abundanz der meisten war

Tabelle 3. Höbäckstjärn-Höbäcken.

Planktonnetz- und Pfahlkratzerproben vom Ufer und von Steinen am Boden.

Kieselalgen	Höbäckstjärn		Höbäcken	
	29.8.1950	18.8.1952	29.8.1950	18.8.1952
Asterionella formosa HASSALL	—	—	+	—
Cymbella aspera EHR. CL.	—	—	r	—
— *cuspidata* KÜTZ.	—	—	+	—
Eunotia exigua (BRÉB.) GRUN.	—	ccc	+	ccc
— *pectinalis* (KÜTZ.) RABH.	+	—	r	—
Frustulia rhomboides v. *saxonica* (RABH.) DE TONI	—	—	r	—
Hantzschia amphioxys (EHR.) GRUN.	r	—	—	—
— *elongata* (HANTZSCH) GRUN.	r	—	r	—
Melosira distans EHR.	r	—	—	—
— *italica* v. *subarctica* O. MÜLL.	r	—	—	—
Navicula lanceolata (AG.) KÜTZ.	—	—	r	—
— *pupula* KÜTZ.	r	—	r	—
Neidium bisulcatum (LAG.ST.) CL.	r	—	—	—
Nitzschia Lanceolatae SPEC.	++	—	+	—
Pinnularia major (KÜTZ.) CL.	—	—	r	—
— *nobilis* EHR.	—	—	r	—
— *nodosa* EHR.	—	—	r	—
— versch. Arten	+	—	—	—
Rhopalodia gibba (EHR.) O. MÜLL.	+	—	r	—
Stenopterobia arctica A. CL.	c	—	r	—
— *intermedia* (LEWIS) FRICKE	r	—	+	—
Synedra ulna v. *biceps* (KÜTZ.) v. SCHÖNF.	—	—	+	—
— kleiner Art	++	—	—	—
Tabellaria fenestrata (LYNGB.) KÜTZ. mit v. *intermedia* GRUN.	+	r	cc	— —
— *flocculosa* (ROTH) KÜTZ.	cc	—	c	—
Tetracyclus lacustris RALFS	—	—	r	—
Versch. kleinere Arten	c	r	++	r

gering. Nur einige wenige Formen kommen zahlreicher vor. Am gewöhnlichsten sind *Tabellaria flocculosa,* eine der häufigsten Kieselalgen in oligodystrophen Seen, und *Anemoeoneis exilis,* die im nördlichen Schweden sehr verbreitet ist. Häufig sind weiter ein paar *Achnanthes*-Arten, unter anderen die nördliche *A. linearis* sowie *Eucocconeis flexella* var. *alpestris,* die beide eigentlich typische Bergformen sind. Ein besonders interessanter Fund ist das zahlreiche Vorkommen der Art *Stenopterobia arctica* A. CL., die man bisher als selten angesehen hat und die nur an wenigen Stellen im schwedischen und finnischen Lappland, sowie als Glacialrelikt in einem See in Dalsland gefunden wurde. Sie ist sehr typisch und leicht von der gewöhnlichen *Stenopterobia intermedia* zu unterscheiden, die auch in einzelnen Exemplaren in diesem See vorkommt. Merkwürdigerweise wurde *Stenopterobia arctica* in keinem Gewässer unterhalb des Höbäckstjärn gefunden. Weiter fand sich eine geringe Zahl von nördlichen und nördlich-alpinen Formen, darunter einige *Achnanthes*-Arten (*A. austriaca, marginulata, Levanderi* und *Peragallii*), *Cymbella hebridica, heteropleura* und *norvegica, Anomoeoneis brachysira, Diploneis Petersenii, Navicula cocconeiformis,* die seltene *Pinnularia undulata* und andere. Weiter kommen eine Anzahl Arten vor, die in Gebirgsgegenden häufig oder sonstwie oligo-dystrophen Charakters sind. Abgesehen von den genannten finden sich in dieser Gruppe unter anderen *Cymbella gracilis, Diploneis finnica, Fragilaria virescens* var. *exigua* und *Fragilaria lapponica, Melosira distans* und *fennoscandica,* einige *Navicula*-Arten (*N. Roteana, subtilissima* und *tridentula*) sowie zahlreiche *Pinnularia*-Arten, unter anderen *Pinnularia Brebissonii, esox, molaris, microstauron, gibba* und *stomatophora.* Die übrigen im Höbäckstjärn verzeichneten Arten sind in ökologischer Hinsicht mehr oder minder indifferent.

Im Höbäcken wurden bei derselben Gelegenheit einige Benthos-Proben mit Pfahlkratzer genommen, die jedoch bezüglich der Kieselalgen nicht so eingehend wie die des Höbäckstjärn untersucht wurden (Tab. 3). Im Bewuchs dominierten die beiden gewöhnlichen *Tabellaria*-Arten, *T. fenestrata* und *flocculosa,* die in grosser Menge vorkommen. Weiter finden sich in lebendem Zustand und in mässiger Anzahl u.a. *Asterionella formosa, Eunotia exigua, Cymbella cuspidata,* kleine *Nitzschia*-Arten, *Synedra ulna* var. *biceps* sowie *Stenopterobia intermedia,* die hier die *Stenopterobia arctica* vom Höbäckstjärn ersetzt. Die übrigen Arten, die in Tab. 3 genannt sind, sind weniger stark vertreten. Zusammenfassend kann man von der ursprünglichen Kieselalgenflora im Höbäckstjärn und Höbäcken sagen, dass sie, obgleich nicht besonders artenreich, doch einen ausgesprochenen Reinwassercharakter hat.

Im August 1952, nachdem das Grubenwasser während eines Jahres in den Höbäckstjärn abgelassen war, hatten sich die Milieu-Verhältnisse in ihm völlig geändert. Die Einwirkung des Grubenwassers auf den See und den Kieselalgenbestand kann als katastrophal bezeichnet werden. Chemische Analysen wurden bei dieser Gelegenheit allerdings nur von den Proben im Höbäcken gemacht. (s. Tab. 2 b.) Frühere Analysen haben aber gezeigt, dass die pH-Werte sowie die Alkalinität des Höbäckstjärns fast dieselben waren wie im Höbäcken, wogegen die Menge der Metalljonen und wahrscheinlich auch der Sulfatjonen im Höbäcken etwas geringer gewesen zu sein scheint. Wie sich aus der Tabelle ergibt, ist der pH-Wert nunmehr enorm — von 7,4 auf 3,2 — gesunken und die Alkalinität ist gleich null. Der Sulfatjonengehalt hat sich auf nicht weniger als 1150 mg/l erhöht. Eisen, Mangan, Kupfer, Zink und Blei erreichen Werte, die das Pessimum der meisten Tiere und Pflanzen weit unterschreitet.

Auch die biologische Untersuchung zeigt, dass die Vernichtung an beiden Probeentnahmestellen so gut wie vollständig ist. Ausser den obengenannten Kieselalgen waren im Jahre 1950 die meisten von den im Süsswasser vorkommenden Pflanzen- und Tiergruppen vorhanden. 1952 fand sich dagegen nichts anderes mehr als einige Flocken, bestehend aus Pilzhyphen, einer festsitzenden Infusorie, ein paar einzelnen Rotatorien und Insektenlarven sowie einer nicht festgestellte, aber in grosser Menge vorkommenden *Sphag-*

num-Art. Gewisse *Sphagnum*-Arten ertragen ja ein stark saures Milieu. Auch die Kieselalgen (Tab. 8) sind, abgesehen von einer »rühmlichen» Ausnahme, verschwunden, wenn man von einzelnen Zellen einiger wenigen Arten im Höbäckstjärn, die aber vermutlich nicht mehr lebten, sowie von einer minderen Anzahl in wenigen Exemplaren vertretener Arten im Oberflächenschlamm des Höbäcken absieht, in dem die Milieu-Bedingungen anscheinend etwas günstiger als im freien Wasser waren. Die erwähnte Ausnahme bildet *Eunotia exigua,* eine Kieselalge, die unten ausführlicher behandelt werden soll. Diese kommt in enormen Mengen als Aufwuchs im Schilfgürtel des Höbäckstjärn und im Oberflächenschlamm des Höbäcken vor. Die Arten, die im Höbäcken aufgezeichnet wurden, bestehen aus Schalen mit nur teilweise bewahrten Chromatophoren, woraus man den Schluss ziehen kann, dass sich auch im Bach keine anderen Kieselalgen über die *Eunotia exigua* hinaus lebend erhalten haben. Das zerstörende Einwirken des Grubenwassers auf Flora und Fauna des kleinen Höbäckstjärn hat sich somit als total erwiesen, sodass kaum eine Möglichkeit bestehen dürfte, die ursprünglichen Verhältnisse, selbst nach späterer Verbesserung der Milieu-Bedingungen durch Einstellung des Abwassers des Anreicherungswerkes, wieder herzustellen.

Das Gillervattnet

Dieser See, der grösste des Wasserwegs, hat ein Areal von ca. 1,2 km^2 und eine grösste Tiefe von 8,3 m. Der Strand ist teils bewaldet, teils besteht er aus Moorboden. In seiner Nähe befinden sich, wenn man von einigen Sommerhäusern absieht, keine festen Bauten. Die chemische Analyse vom September 1950, Tab. 4, zeigt, dass das Gillervattnet einen ähnlichen Charakter wie der Höbäckstjärn hatte. Es ist in Bezug auf seinen Säuregrad fast völlig neutral und hat ungefähr gleich niedrige Werte an SO_4, Fe, Mn, Pb und Zn.

Das biologische Material besteht sowohl aus Planktonproben vom freiem Wasser und vom Strand, als auch aus Proben aus dem Oberflächenschlamm des Bodens. Die Planktonproben, Tab. 5, sind bezüglich der Kieselalgen ziemlich artenarm, aber desto reicher an Individuen. Es kommen grosse Mengen von hauptsächlich *Melosira ambigua* und *Tabellaria fenestrata* var. *lacustris* vor. Auch *Asterionella formosa* und *Fragilaria capucina* treten ziemlich häufig auf, weiter in geringerer Zahl auch *Melosira italica* var. *valida* und *Tabellaria flocculosa.* Dazu finden sich einzelne Exemplare von verschiedenen Kieselalgen, hauptsächlich Benthosformen, die, von ihrer Unterlage losgerissen, im Plankton nur zufällig vorkommen. Wenn auch ausserhalb des Rahmens dieser Untersuchung liegend, mag zur Beleuchtung des oligotrophen Charakters des Sees angeführt werden, dass die übrige biologische Untersuchung ebenfalls keinen grösseren Artenreichtum ergeben

Tabelle 4. Gillervattnet. Chemische Analyse.

Datum	Trübung $^0ZPlO^5$	pH	Alkal. ln. HCl/l	SO_4 mg/l	Fe mg/l	Mn mg/l	Cu mg/l	Pb mg/l	As mg/l	Zn mg/l
26.9.—50	—	7,3	0,23	4,0	0,27	0,1	—	0,05	—	0,05
19.8.—52	125	4,2	0	130,0	0,7	1,5	0,45	0,14	0,05	3,5
8.8.—53	155	3,6	0	222,0	0,5	3,1	0,03	0,3	0,01	6,3
17.3.—54	195	4,0	0	230,0	2,3	2,1	0,5	0,21	$< 0,05$	6,3

haben. Quantitativ herrschen sowohl betr. Arten- als auch Individuenanzahl die Cyanophycéen vor, die in Nordschweden zu dieser Zeit ihr Maximum erreichen. Ferner finden sich reichlich *Dinobryon divergens,* ziemlich viele Desmidiéenarten sowie ziemlich zahlreich zu der Gruppe der Tetrasporalen gehörende Chlorococcalen (*Asterococcus superbus, Tetraspora lacustris, Paulschultzia pseudovolvox*); letztere sind alle typisch für oligotrophe Seen. Die übrigen Chlorococcalen kommen nur in geringer Anzahl vor. Selbst das Zooplankton weist eine geringe Artenanzahl, und zwar fast ausschliesslich aus der Rotatorien- und Cladoceren-Gruppe, sowie eine einzige Copepodenart auf.

Die Kieselalgenprobe vom Oberflächenschlamm des Bodens ist reich an Arten der verschiedenen Biotopen des Sees. Insgesamt wurden 219 Arten, Varieteten und Formen aufgezeichnet. Im Gegensatz zum Höbäckstjärn findet sich im Bodenschlamm dieses grösseren Sees eine Menge von Schalen und noch lebenden Zellen, die der Planktonflora des Sees angehören. Unter ihnen sind besonders *Melosira ambigua* und *Tabellaria fenestrata* zahlreich, sowie *Cyclotella comta,* die indessen nicht in merkbaren Mengen in der Planktonprobe vorkommen. *Asterionella formosa* dagegen, die in der Planktonprobe ziemlich zahlreich ist, wurde zu dieser Zeit in der Bodenprobe nicht festgestellt. Von den zahlreichen Benthosformen findet man eine Menge der oligo-dystrophen Arten, die den Höbäckstjärn charakterisierten, sowie die mehr nördlichen und nördlich-alpinen Arten dieses Sees, besonders innerhalb der *Achnanthes-* und *Pinnularia*-Gruppen. Innerhalb letzterer kommen jedoch mehrere Arten hinzu, die sich im Höbäckstjärn-Höbäcken nicht finden. Von diesen seien genannt: *Cymbella Suecica, Diploneis Boldtiana,* einige *Eunotia*-Arten (*E. faba, pectinalis* mit var. *constricta, robusta*-Varieteten sowie *valida*), weiter *Frustulia amphipleuroides, Melosira lirata* und *Melosira italica* var. *valida* sowie *Melosira undulata* mit var. *Normanni.* Die beiden letzteren sind typisch dystrophe Seeformen. Weiter finden sich verschiedene *Pinnularia*-Arten, die auch für oligo-dystrophe Gewässer charakteristisch und in diesem See zum Teil sehr zahlreich vertreten sind. Unter ihnen verdienen Aufmerksamkeit besonders *Pinnularia acrosphaeria, hemiptera* und *nobilis,* sowie einzelne Exemplare von *Pinnularia dactylis, divergens, karelica, lata,* die sehr seltene *Pinnularia major* var. *transversa* sowie *P. mesogongyla.* Die meisten Arten dieses Sees sind indessen nach ihrem öko-

Tabelle 5. Gillervattnet mit Abflussbach.

Planktonnetzproben im freien Wasser und in der Uferregion.
Pfahlkratzerproben vom Uferschilf und von Steinen am Boden.

Kieselalgen	Gillervattnet				Abflussbach	
	Freies Wasser		Ufer		1950 29.8.	1952 18.8.
	1950 29.8.	1952 18.8.	1950 29.8.	1952 18.8.		
Asterionella formosa HASSALL	++	r	++	—	—	—
Cymbella aspera (EHR.) CL.	—	—	—	—	+	—
— *hybrida* GRUN.	—	—	—	—	+	—
— *lanceolata* (EHR.) V. H.	—	—	+	—	+	—
Eunotia pectinalis (KÜTZ.) RABH.	—	—	+	—	++	—
— *exigua* (BRÉB.) GRUN.	—	++	—	cc	—	cc
Fragilaria capucina DESMAZ.	++	—	++	—	c	—
— *construens* v. *venter* GRUN.	—	—	—	—	+	—
— *elliptica* V. H.	—	—	+	—	—	r
Melosira ambigua (GRUN.) O. MÜLL.	cc	+	c	—	++	+
— *italica* v. *valida* GRUN.	+	rr	—	—	—	—
— *undulata* KÜTZ.	r	r	—	—	—	—
Pinnularia major (KÜTZ.) CL.	—	—	+	—	—	+
— *nobilis* EHR.	—	—	—	—	+	—
— *viridis* (NITZSCH.) EHR.	—	—	—	—	—	r
Rhopalodia gibba (EHR.) O. MÜLL.	—	—	+	—	+	—
Synedra ulna (NITZSCH.) EHR.	—	—	—	—	+	—
Tabellaria fenestrata (LYNGB.) KÜTZ. v. *lacustris* MEIST.	cc	r	cc	—	++	—
— *flocculosa* (ROTH) KÜTZ.	+	—	—	—	—	—
Tetracyclus lacustris RALFS	—	—	+	—	—	r
Schalen versch. Benthosformen	+	—	—	+	—	++

logischen Charakter indifferent und eurytop, eine geringe Anzahl ist sogar rein alkaliphil und eutroph. Unter den letztgenannten befinden sich *Amphora ovalis,* eine Anzahl *Cymbella*-Arten, (*C. aspera, cistula, Ehrenbergii, suecica* und *turgida*), *Eunotia gracilis, Fragilaria construens* mit var. *venter.* Andere in Seen gewöhnliche, alkaliphile *Fragilaria*-Arten sind *Fragilaria brevistriata* sowie in auffallender Menge *Fr. pinnata* und *elliptica.* Aus der gleichen ökologischen Gruppe von hauptsächlich indifferentem Charakter kommen *Gyrosigma acuminatum* und eine grosse Anzahl *Caloneis- Gomphonema- Navicula- Neidium* und *Nitzschia*-Arten vor. Typische Bodenformen sind die in grösseren Seen gewöhnliche *Campylodiscus noricus* var. *hibernica,* die spärlich vorkommt, sowie die stärker vertretene *Surirella robusta* mit ihren Variationen. Alle diese Formen fehlen oder sind selten im Höbäckstjärn. Der See Gillervattnet kann also auf Grund seiner bedeutend grösseren freien Wasseroberfläche eine Anzahl Arten von mehr planktischem Charakter beherbergen. Die Artzusammensetzung der Proben des Jahres 1950 zeigt zusammen mit den übrigen biologischen Funden sowie den chemischen Werten, die bei dieser Gelegenheit festgestellt wurden, einen oligotrophen Klarwassersee von mehr temperiertem, als typisch nordischem Charakter.

Bei der Probeentnahme, die 2 Jahre später im August stattfand, war auffallend, dass die schädliche Wirkung des Grubenwassers auf Grund der stärkeren Verdünnung in diesem See nicht den gleichen vernichtenden Umfang erreicht hatte wie im Höbäckstjärn. Die chemische Analyse, Tab. 4, zeigt, dass der pH-Wert immer noch ziemlich niedrig und die Alkalinität auch hier gleich null, dass aber die Menge der giftigen Jonen bedeutend reduziert ist. Die Verunreinigung war aber immerhin so gross, dass sie, wie die Planktonproben Tab. 5 zeigen, fast das ganze organische Leben im pelagischen Teil des Sees ausgerottet hat. Von der individuenreichen Planktonflora, die früher im See vorhanden war, finden sich in lebendem Zustand nur noch einzelne Zellen von *Melosira ambigua,* sowie einige wenige andere Plankton-Arten. Die einzige Art, die auch hier weiter gedeiht, ist *Eunotia exigua,* die in ziemlich grosser Anzahl, gebunden an die kleinen, schwebenden *Detritus*-Flocken und als Aufwuchs auf losgerissenen Algenfäden vorkommt. Im Bodenschlamm, Tab. 8, sind die Kieselalgen aber weiterhin sehr zahlreich vorhanden, obgleich sich nur noch wenige Arten in lebendem Zustand oder zumindesten unter Beibehalt der Chromatophoren finden. Dieses gilt besonders für *Melosira ambigua,* die die dominierende Form auch im Schlamm ist, wo sie anscheinend üppig gedeiht auch wenn sie im Plankton verschwunden ist. Die gleiche Beobachtung konnte früher in einem anderen stark acidotrophen See, dem Sladan in Norrbotten, gemacht werden, wo diese *Melosira* in lebendem Zustand und in viel grösserer Zahl im Bodenschlamm als in dem stark sauren freien Wasser (pH=3,7) vorkommt. Abgesehen von *Melosira ambigua* finden sich unter den lebenden Arten im Oberflächenschlamm des Gillervattnet sehr zahlreich *Melosira undulata,* sowie recht häufig eine kleine *Fragilaria,* wahrscheinlich *elliptica,* sowie *Eunotia exigua.* Letztgenannte, die nur in einigen Exemplaren in der Schlammprobe von 1950 auftritt, ist nun zahlreich vertreten, obgleich bei weitem nicht so dominierend wie im Höbäckstjärn. Im übrigen ist die Artenanzahl im Bodenschlamm auf ungefähr $^1/_3$ der Anzahl des Jahres 1950 gesunken. Einige Arten sind zahlenmässig zurückgegangen, andere, darunter die nördlich-alpine *Surirella helvetica,* die sich früher ganz zahlreich fand, fehlen völlig. Weitere Formen wiederum erreichen in der Probe von 1952 eine grössere Abundanz, z.B. — ausser *Eunotia exigua* — die azidophile Seeform *Melosira undulata,* die schon im Jahre 1950 zahlreich auftrat, nun aber zu den deutlich dominierenden Formen gehört.

Ein Vergleich zwischen dem Kieselalgenbestand der Probe von 1950 mit dem der Probe von 1952 zeigt also, dass die schädliche Einwirkung des Grubenwassers selbst in diesem See so gross war, dass der Bestand in seinen pelagischen Teilen so gut wie völlig ausgerottet wurde, während es in den oberen Teilen des Bodenschlamms einer geringen Anzahl von Formen zu überleben glückte und eine ziemlich grosse Anzahl von Schalen erhalten blieb.

Auch von dem Aufwuchs im Abflussbach des Gillervattnet wurde im September 1952 eine Probe genommen, aber leider wurde keine chemische Analyse gemacht. Die Probe ist vollständig von *Eunotia exigua* beherrscht, die mindestens 90 % des Algenbestandes ausmacht. Es ist interessant zu sehen, wie diese Kieselalge aufblüht, sobald die Milieu-Bedingungen für sie passend, d.h. so »schlecht» werden, dass alle anderen Arten ausser ihr verschwinden. Diese *Eunotia exigua* (BRÉB.) GRUNOW ist so eigentümlich und interessant in ihrem Auftreten, dass sie besondere Aufmerksamkeit verdient. In den Proben von 1950 kam sie nur sparsam an mehreren Stellen vor, etwas zahlreicher in einer Probe vom Steinbewuchs am Boden des Höbäcken. Im Höbäckstjärn wurden nur einzelne Exemplare gefunden. Umso auffallender ist die Veränderung im Auftreten der Alge nach 2 Jahren. Wie schon erwähnt, ist sie im Höbäckstjärn praktisch die einzige vorkommende Kieselalge, im Höbäcken die klar dominierende Form, und sie kommt noch im Plankton des Gillervattnet, und zwar als dominierende Form an flacheren Stellen bis hinab in den zuletzt erwähnten Abflussbach vom Gillervattnet vor. Wie wir sehen werden, ist sie auch im Bruträsket als Bewuchsform in der Strandvegetation gewöhnlich. In einer früheren Arbeit (STJERNA-POOTH 1953) habe ich ein Massenauftreten dieser Alge unter ähnlichen ökologischen Verhältnissen, nämlich in einem stark schwefelsauren See, dem Blåmisutjärn im Küstenbereich von Norrbotten, beschrieben. In ihm kam, bei einem pH-Wert von 3,1 in dem freien Wasser, *Eunotia exigua* als einzige Form in unerhörten Mengen, besonders in seinen flacheren Teilen als Aufwuchs auf *Sphagnum Dusenii* vor, und sogar im Plankton war sie sehr zahlreich. Gelegentlich der Probeentnahme von 1952 in den Boliden Seen war der pH-Wert im Höbäcken 3,2 und der Sulfatjonenwert 1150 mg/l. Soweit stimmen die Verhältnisse im Blåmisutjärn und Höbäckstjärn-Höbäcken überein. Hinzu aber kommen im Abwasser der Bolidengrube die vielen giftigen Metallsalze, und es fragt sich, welcher oder welche Faktoren bestimmend für die enorme Entwicklung der Alge sind: der niedrige pH-Wert, die SO_4-Jonen oder das Fehlen jeglicher Konkurrenz mit anderen Formen. Dass sie das Vorkommen einer Menge giftiger Jonen aushält, zeigt wohl nur, dass sie ausserordentlich widerstandskräftig gegen diese Einflüsse ist. In der Litteratur wird die Ökologie von *Eunotia exigua* an verschiedenen Stellen behandelt. JÖRGENSEN (1948) hat sie als dominierende Form in einer *Sphagnum*-Probe und in geringerer Anzahl in oligotrophen Seen gefunden. Er bezeichnet sie als eine azidobionte Form, die bei pH=4.0—5,0 zahlreich, aber auch bei pH < 4,0 gefunden wird. Dagegen wollen weder er noch BOYE-PETERSEN (1950) sie im Gegensatz zu früheren Annahmen als eine typisch sphagnophile Form gelten lassen. Dieses wird auch durch unsere Proben bestätigt. Gewiss tritt die Alge im Blåmisutjärn auf einer Unterlage des eben erwähnten *Sphagnum* auf, aber im Höbäckstjärn ist sie an andere Unterlagen gebunden, nämlich an die Schilf- und Carex-Vegetation des Strandes, sowie die obersten Schlammlager des Bodens. Hier wurde sie, in grünen Klumpen zusammengebacken, in grossen Mengen lebend erhalten. HUSTEDT (1938) bezeichnet sie als oligohalob und wenig empfindlich gegen veränderte Konzentrationen. Es ist möglich, dass gerade der niedrige pH-Wert ein wesentlicher Faktor für das Wohlbefinden der *Eunotia* ist, jedenfalls kann man wohl mit Sicherheit behaupten, dass weder ein extrem niedriger pH-Wert, noch sogar Mengen giftiger Metallsalze (welche Faktoren zusammen und schon für sich allein die Existenz anderer Kieselalgen ausschliessen) hemmende Wirkungen auf diese Alge ausgeübt hat.

HUSTEDT hebt ferner ihre starke Tendenz zu morphologischen Variationen in saurem Wasser hervor. Ein Vergleich der Fig. 2—4 bestätigt dieses. Fig. 2 zeigt *Eunotia exigua* im Höbäckstjärn 1952. Vorherrschend ist eine kleine, »knollige» Form mit einer Länge von 13—17 μ und einer Breite von 3,5— 4 μ. Es kommen aber auch einige längere Zellen vor, die zusammen etwa 2—3 % der Gesamtzahl bilden. Deren Länge beträgt 30—35 μ bei einer Breite von 3—3,3 μ. Die Anzahl der Streifen ist dieselbe, nämlich 21—22 auf 10 μ. Im Höbäcken sind, wie Fig. 3 zeigt, die Verhältnisse zwischen den beiden Formen zahlenmässig ca. 1 : 1. Auch Übergangsformen sind erkennbar, aber sie sind nicht zahlreich. Vorherrschend sind eine kurze Form und eine, die ungefähr doppelt so lang ist. Ob nun die morphologischen Verschiedenheiten durch die etwas verschiedenen chemischen Milieuverhältnisse an den beiden Probeentnahmestellen bedingt sind, oder ob es sich um verschiedene Entwicklungsstadien der Alge handelt, also um einen Altersunterschied, ist wohl nicht leicht zu beantworten. Vielleicht kann der grosse Prozentsatz verkrüppelter Formen im Höbäckstjärn dahin gedeutet werden, dass auch *Eunotia exigua* nicht unbegrenzte Mengen von Gift aushält. Das Foto Fig. 4, das zu Vergleichszwecken mitgenommen wurde, zeigt die *Eunotia exigua* im Blåmisutjärn. Die Länge der Alge variiert hier zwischen 13 und 45 μ. Die meisten Exemplare halten sich zwischen 35 und 40 μ und die Breite ist 2,9—3 μ. Die Exemplare sind also etwas schmaler als in den Bolidenseen, wogegen die Anzahl der Streifen mit 21—22 auf 10 μ die gleiche ist. Die Zellenenden scheinen oft dorsal etwas mehr abgerundet.

Bezüglich der Nomenklatur variieren die Angaben in der Diatomaceenlitteratur nicht weniger als die Alge selbst. Der Einfachkeit halber habe ich hier die Art, die in den Bestand sowohl des Blåmisutjärn als auch der Bolidenseen eingeht, recht und schlecht *Eunotia exigua* (BRÉB.) GRUNOW sensu HUSTEDT 1932 genannt. Nach BOYE-PETERSEN (1950) scheint die typische *Eunotia exigua* entsprechend der Ansicht GRUNOWS etwas feinstreifiger (24 Streifen auf 10 μ) und durchschnittlich sowohl kürzer als schmaler (l=10—26 μ, br.=2,5—3,3 μ) als unsere Exemplare der norrländischen Seen zu sein. Tatsächlich stimmen diese in manchen Einzelheiten besser überein mit einer Beschreibung der *Eunotia Nymanniana* GRUNOW, die ASTRID CLEVE (1953) in ihrem Werk »Die Diatomeen von Schweden und

Fig. 2. *Eunotia exigua* im Höbäckstjärn, Aug. 1952.

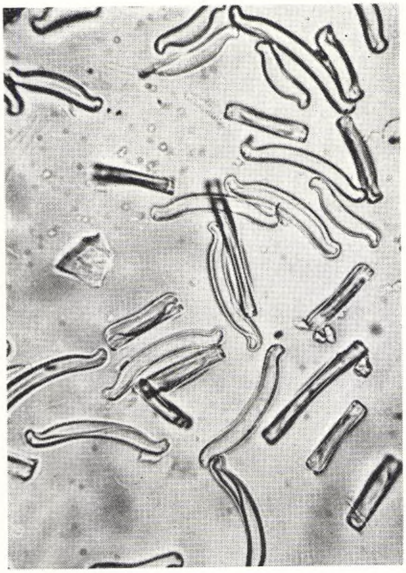

Fig. 3. *Eunotia exigua* im Höbäcken. Aug. 1952.

Fig. 4. *Eunotia exigua* im Blåmisutjärn, Sept. 1952.

Finnland» wiedergibt. Diese Verfasserin meint, dass die authentische *Eunotia exigua* bei uns und besonders in Lappland seltener ist als *Eunotia Nymanniana*. Vielleicht wäre es deshalb richtiger, die hier gefundene *Eunotia*-Art *Eunotia Nymanniana* zu nennen. Trotzdem habe ich den Namen *Eunotia exigua* in weiterem Sinne gewählt.

Der See Bruträsket

Der dritte der Seen im Gillerwasserweg, der Bruträsket, hat eine Flächenausdehnung von nur ungefähr 0.35 km^2. Er wird durchströmt von dem Brubäcken, der einige kleine Seen westlich des Wasserwegs entwässert, und der sich etwa 3 km nach seinem Ausfluss aus dem Bruträsket in den Skellefte-Älv ergiesst. Der Brubäcken fliesst durch unbebaute Sumpfmarken, und auch die Umgebung des Bruträsket ist zum grössten Teil unbebaut. Vor 1951 fehlte dem Bruträsket eine Verbindung mit dem Gillervattnet, die er, wie erwähnt, erst im Zusammenhang mit dem Ablassen des Grubenwassers durch Herstellung eines 1,5 km langen Grabens zwischen dem Brubäcken und einem künstlichen Damm im Gillervattenbach erhielt, welch letzterer den natürlichen Ablauf des Gillervattnet in westlicher Richtung bildet.

Die chemische Beschaffenheit seines Wassers vor dem Ablassen des Grubenwassers gleicht, wie aus Tab. 6 hervorgeht, in hohem Masse der in den zuvorgenannten Seen. Der pH-Wert 7,3 ist identisch mit dem pH-Wert im Gillervattnet. Die Alkalinität ist fast die gleiche, ebenso sind die Jonen-Werte fast gleich, woraus sich ergibt, dass der Bruträsket in ökologischer Hinsicht einen oligotrophen Charakter mit reinem und klarem Wasser hat. Dieses wird wiederum bestätigt durch die Zusammensetzung der Planktonprobe von 1950 (Tab. 7). Die dominierende Kieselalge ist *Asterionella formosa* in grossen Mengen, sowie *Tabellaria fenestrata,* von der besonders die var. *asterionelloides* sehr zahlreich auftritt. Auch *Cyclotella comta* ist recht häufig im freien Wasser, ebenso wie *Melosira italica* var. *ambigua,* sowie verschiedene mehr zufällig im Plankton auftretende Benthosformen. Unter diesen ist im Oberflächenschlamm (Tab. 8) ein deutlicher Einschlag der azidophilen, sowie der nördlichen und nördlich-alpinen Klarwasserformen festzustellen. Abgesehen von mehreren Formen, die dieser See mit den vor-

Tabelle 6. Bruträsket. Chemische Analyse.

Datum	Trübung ^{0}ZPlO^5	pH	Alkal. ln. HCl/l	SO$_4$ mg/l	Fe mg/l	Mn mg/l	Cu mg/l	Pb mg/l	As mg/l	Zn mg/l
26.9.—50		7,3	0,24	5,0	0,9	0,1		0,05		0,05
19.8.—52	155	5,8	0,16	29,0	0,30	0,08	0,05	0,05	0,05	0,2
8.8.—53	275	5,4	0	64,0	0,3	1,0	0,03	0,16	0,01	0,9

Tabelle 7. Bruträsket.

Planktonnetzproben im freien Wasser und in der Uferregion.
Pfahlkratzerproben in der Ufervegetation.

Kieselalgen	Freies Wasser		Ufer	
	1950	1952	1950	1952
Asterionella formosa Hassall	cc	—	cc	—
Cyclotella comta (Ehr.) Kütz.	++	—	—	—
Eunotia pectinalis (Kütz.) Rabh.	r	—	c	—
— *exigua* (Bréb.) Grun.	—	—	—	++
Fragilaria spec.	+	—	—	—
Melosira italica v. *ambigua* (Grun.) O. Müll.	+	rr	r	—
— *italica* v. *valida* Grun.	r	—	+	—
Rhopalodia gibba (Ehr.) O. Müll.	r	—	r	—
Stenopterobia intermedia (Lewis) Fricke	+	+	r	++
Tabellaria fenestrata (Lyngb.) Kütz. v. *asterionelloides* Grun.	c	rr	c	+
— — v. *intermedia* Grun.	—	—	+	—
— — v. *lacustris* Meist.	—	—	++	—
— *flocculosa* (Roth) Kütz.	—	—	r	r
Versch. Benthosformen	r	r	—	—
Schalen versch. Plankton-Arten	—	—	—	++

herbehandelten gemeinsam hat, konnten verschiedene neue festgestellt werden, besonders in den Gruppen *Cymbella* (*C. amphioxys, incerta, perpusilla, obtusa*), *Eunotia* (*E. alpina, lunaris* mit var. *subarcuata, Nymanniana, pectinalis* var. *undulata, praerupta* mit var. *laticeps, septentrionalis*) sowie *Pinnularia* (*P. appendiculata, Brandelii, Braunei, streptoraphe* mit var. *styliformis, isostauron, brevicostata* sowie die auch im Höbäckstjärn gefundene seltene *P. undulata*). *Frustulia saxonica* und *Stenopterobia intermedia* sind hier häufiger als in den anderen Seen. Besonders die letztgenannte Art ist sehr gewöhnlich. Ich war etwas im Zweifel ob ich sie unter die Hauptart *intermedia* oder unter die in Schweden nicht ungewöhnliche Variation *capitata* einordnen sollte. Tatsächlich scheint sie eine Mittelform zu sein. Im Gegensatz zu der Hauptform behält sie meistens ihre Breite (ca. 8 μ) bis zu den Enden, die leicht konisch abgerundet, jedoch nicht angeschwollen sind wie bei der var. *capitata*. Vielleicht handelt es sich um eine neue Varietät. Da die Diatomacéen-Litteratur aber schon mit Formen und Variationen genügend belastet ist, habe ich davon abgesehen, sie als neu einzuführen, und sie in meiner Liste der Hauptform hinzugerechnet. Schliesslich kann von der Kieselalgenflora im Bruträsket 1950 bemerkt werden, dass die mehr eutrophen und indifferenten Formen, die im Gillervattnet auftreten, hier nicht die gleiche Zahl und den gleichen Individuenreichtum aufweisen.

Hinsichtlich der Verhältnisse 2 Jahre später geht aus der chemischen Analyse (Tab. 6) hervor, dass das Grubenabwasser im Bruträsket eine so starke Verdünnung erreicht hat, dass sich die chemischen Werte hier den normalen annäherten. Die giftigen Kupfer- und Bleisalze kamen nur spärlich vor. Zn, Mn und Fe haben die niedrigen Werte von 0,2, 0,08 und 0,3

Tabelle 8. Kieselalgen aus dem Plankton und Aufwuchs im Höbäckstjärn samt aus dem Bodenschlamm im Höbäcken, Gillervattnet und Bruträsket.

	Höbäcks-tjärn		Hö-bäcken	Giller-vattnet		Bruträsket	
	1950	1952	1952	1950	1952	1950	1952
Achnanthes austriaca Hust.	r						
— — v. *helvetica* Hust.	r						
— *biasolettiana* Kütz.				+	+	+	+
— *delicatula* (Kütz.) Grun.				r	r		
— *didyma* Hust.				r		r	r
— *exigua* Grun.				r			
— — v. *heterovalvata* Krasske					r		
— *hungarica* Grun.	r						
— *lanceolata* (Bréb.) Grun.	r			r			
— *laterostrata* Hust.				+	+		r
— *latissima* A. Cl.				r			
— *marginulata* Grun.	r	rr	r	r	r		
— *microcephala* Kütz.	r			r	r	+	+
— *minutissima* Kütz.	c		+	cc	r	c	c
— *Levanderi* Hust.	r			r	r		r
— *linearis* (W. Sm.) Grun.	c			} c		} ++	} ++
— — v. *pusilla* Grun.	r		r		+		
— *Peragallii* Brun u. Her.	r			+	+		
— *Östrupii* A. Cl.				r	r		
— spec. wenigst. 2 Art.			r	r			
Amphicampa hemicyclus Ehr.							rr
Amphipleura pellucida Kütz.				r			
Amphiprora ornata v. *rectangulata* A. Cl.						r	r
Amphora libyca Ehr.	++			++	++	+	+
— *ovalis* Kütz.	r			+	+	+	+
— — f. *gracilis* Ehr.				r			
— — v. *pediculus* Kütz. f. *minor* V. H.				r			
Anomoeoneis brachysira (Bréb.) Grun.			r	r		++	+
— *exilis* (Kütz.) Cl.	cc	r	r	r		+	++
— *zellensis* (Grun.) Cl.							r
Asterionella formosa Hassall							++
Caloneis bacillum (Grun.) Mereschk.				r	r	r	r
— *bacillaris* v. *lacun.* Grun.							r
— *obtusa* (W. Sm.) Cl.				r	r		
— *silicula* (Ehr.) Cl.				+	r	r	
— — v. *gibberula* (Kütz.) Grun.							r
— — v. *ventricosa* (Ehr.) ? Donk.	r						
— *Schumanniana* v. *biconstricta* Grun.				r	r	r	
Campylodiscus noricus v. *hibernica* (Ehr.) Grun.				r	r	r	r
Cocconeis placentula Ehr.				r	r		
— — v. *lineata* (Ehr.) Cl.				r			
— — v. *euglypta* (Ehr.) Cl.				r			
— — v. *klinoraphis* Geitler				r			
Cyclotella compta (Ehr.) Kütz.	r			c	c	++	c
— — v. *radiosa* Grun.						r	
— *Kützingiana* v. *planetophora* Fricke						r	r
— — v. *radiosa* Fricke Schm.						r	r
— *Meneghiniana* v. *rect.* Grun.						r	r
— *stelligera* Cl. u. Grun.						++	++
Cymbella amphicephala Naeg.	r			r		r	+
— *amphioxys* (Kütz.) Grun.						r	r
— *angustata* (W. Sm.) Cl.	r					+	+
— *aspera* (Ehr.) Cl.				+	+	+	r
— *cesati* Grun.	r						

Tabelle 8. Forts.

	Höbäckstjärn		Höbäcken	Gillervattnet		Bruträsket	
	1950	1952	1952	1950	1952	1950	1952
— *cistula* (HEMPR.) GRUN.				+	+	r	r
— — v. *maculata* (KÜTZ.) V. H.				r	r		
— *cuspidata* KÜTZ.				r		r	
— *cymbiformis* (KÜTZ.) V. H.				r	r		
— *Ehrenbergii* KÜTZ.			r	r	r		
— *gracilis* (RABH.) CL.			r	r		+	+
— *hebridica* (GREG.) CL.			r	r	r	+	+
— *helvetica* KÜTZ.	r			r	r		
— *heteropleura* v. *minor* CL.			r	r	r	r	
— *hybrida* GRUN.	r						r
— *incerta* GRUN.						r	
— *lanceolata* (EHR.) V. H.				+	+		
— *microcephala* GRUN.				r	r	+	r
— *naviculiformis* AUERSW. HUST.			r	r	r	r	r
— *norvegica* GRUN.	r						
— *obtusa* GREG.						r	
— *parva* (W. SM.) CL.				+			
— *perpusilla* A. CL.						r	r
— *sphaerophora* A. CL.				r		r	
— *suecica* A. CL.				+	+	++	++
— *tumida* (GREG.) V. H.				r	r		
— *turgida* (GREG.) CL.				+	+	++	++
— *ventricosa* KÜTZ.				r		r	
— — v. *caespitosa* KÜTZ.	r			r	r		r
Cymatopleura solea (BRÉB.) W. SM.				r	r		
Denticula tenuis v. *inflata* (W. SM.) GRUN.				r			
Diatoma elongatum AGARDH				r			
Diploneis Boldtiana CL.				r	r	r	r
— *carpathorum* (PANT.) A. CL.				r			
— *elliptica* (KÜTZ.) CL.				++	++	+	++
— *finnica* (EHR.) CL.	r			++	++	r	+
— *oculata* (BRÉB.) CL.	r			r		r	+
— *ovalis* (HILSE) CL.						r	
— — v. *oblongella* (NAEG.) CL.						r	
— *Peterseni* HUST.			r				
Epithemia sorex KÜTZ.	r						
— *zebra* (EHR.) KÜTZ.				++	r		
— — v. *porcellus* (KÜTZ.) GRUN.				r	r		
Eucocconeis flexella (KÜTZ.)						r	} +
— — v. *alpestris* BRUN.	c					r	
— *lapponica* HUST.			r				
Eunotia alpina (NAEG.) HUST.						r	
— *arcus* EHR.						r	
— *bidentula* W. SM.	r					r	r
— *exigua* (BRÉB.) GRUN.	rr	ccc	cc	r	c	r	r
— *faba* (EHR.) GRUN.				r		+	+
— *flexuosa* (BRÉB.) KÜTZ.						+	r
— *formica* EHR.	r			r	r	r	
— *gracilis* (EHR.) RABH.				r		+	
— *impressa* v. *angusta* GRUN.				r			
— *lunaris* (EHR.) GRUN.						+	r
— — v. *subarcuata* (EHR.) GRUN.						r	
— *Nymanniana* GRUN.						r	
— *pectinalis* (KÜTZ.) RABH.				++		+	} ++
— — v. *biconstricta* GRUN.				r	r	+	
— — v. *minor* (KÜTZ.) RABH.			r	r	r	+	
— — v. *undulata* RALFS	r					r	

Tabelle 8. Forts.

	Höbäckstjärn		Höbäcken	Gillervattnet		Bruträsket	
	1950	1952	1952	1950	1952	1950	1952
— *polyglyphis* Grun.							r
— *praerupta* mit v. *laticeps* Grun.						+	+
— *robusta* v. *diadema* (Ehr.) Ralfs				r	r	r	
— — v. *tetraodon* (Ehr.) Ralfs				r	r	+	+
— *scandinavica* A. Cl.				r			
— *septentrionalis* Östr.							r
— *tridentula* (Ehr.) Å. Bg.						r	
— *valida* Hust.				r	r		r
— *veneris* (Kütz.) O. Müll.				r		+	+
— — v. *obtusiuscula* Grun.						r	
— spec.		rr	r		r		r
Fragilaria brevistriata Grun.				+	++		
— *capucina* Desmaz.				+			
— *constricta* Ehr.						r	
— *construens* (Ehr.) Grun.				c	c	+	+
— — v. *venter* Grun.						++	++
— — v. *binodes* Grun.				r		r	
— *elliptica* V. H.	r			c	c		
— *Heidenii* Östr.				r	r		
— *lapponica* Grun.							
— *pinnata* Ehr. mit var.				++	++	+	+
— *virescens* Ralfs	r			r	r	++	++
— — v. *exigua* Grun.	r					+	+
— — v. *oblongella* Grun.						+	
— — v. *mesolepta* Rabh.							+
Frustulia amphipleuroides Grun.				r	r		
— *rhomboides* de Toni						+	r
— — v. *saxonica* (Rabh.) de Toni			r	r	r	++	++
— *vulgaris* Twaites			r				
Gomphonema acuminatum Ehr.				r		r	
— — v. *Brebissonii* Kütz.	r			r			
— — v. *coronata* (Ehr.) W. Sm.				+	r	r	r
— — v. *Pantocsekii* A. Cl.	r			r	r		
— *angustatum* (Kütz.) Rabh.							r
— — v. *linearis* Hust.			r				
— *apicatum* Ehr.				r			
— *augur* v. *Gautieri* V. H.				r			
— *elongatum* (Ehr.) W. Sm.				r	r		
— *gracile* Ehr.				r	r		r
— — v. *aurita* (A. Braun) Cl.				r		+	
— *intricatum* v. *dichotoma* (Kütz.) Grun.				r			
— — v. *pumila* Grun.				r			
— *montanum* Schum.						r	
— *micropus* Kütz.				r			
— *olivaceum* (Ehr.) Lyngb.				r			
— *parvulum* (Kütz.) Grun.				r			
— *subtile* Ehr.						r	
— — v. *sagitta* (Schum.) Cl.						r	r
— *subulatum* A. Cl.				r			
Gyrosigma acuminatum (Kütz.) Rabh.				+	+	r	+
— — v. *gallica* Grun.				r	+		
Hantzschia amphioxys (Ehr.) Grun.	r					r	
— *elongata* (Hantzsch) Grun.	r			r	r	r	r
Melosira ambigua (Grun.) O. Müll.				cc	cc	++	++
— *arenaria* Moore					rr		
— *distans* Ehr.	r					++	++

Tabelle 8. Forts.

	Höbäcks-tjärn		Hö-bäcken	Giller-vattnet		Bruträsket	
	1950	1952	1952	1950	1952	1950	1952
— — v. *humilis* A. Cl.				+	+		+
— — v. *lirata* (Ehr.) Bettge				++	++	c	++
— — v. f. *lacustris* Grun.						+	+
— *fennoscandica* A. Cl.	r			+	++	+	++
— *granulata* (Ehr.) Ralfs						r	
— *italica* v. *valida* Grun.				+	+	cc	c
— *undulata* Kütz.				++	cc		
— — v. *Normanni* Arn. M.							
Navicula americana Ehr.						r	r
— *anglica* Ralfs	r			r	r	r	
— *bacilliformis* Grun.	r			+	r	r	
— *bacillum* Ehr.				r	r		r
— *cocconeiformis* Greg.	r					+	+
— *cryptocephala* Kütz.	r		r		r	++	+
— — v. *intermedia* Grun.				r	r	+	+
— — v. *veneta* (Kütz.) Grun.	r			r			
— *cuspidata* Kütz.						r	
— *dicephala* (Ehr.) W. Sm.					+	+	++
— *elginensis* (Greg.) Grun.						r	
— *exigua* (Greg.) O. Müll.				r	+		r
— cfr *festiva* Krasske				r	r		
— *gastrum* Ehr. Cl.							r
— *hassiaca* Krasske	r						
— *Jentzschii* Grun.	r						
— *lanceolata* (Ag.) Kütz.				r		+	r
— *laterostrata* Hust.				r			r
— cfr *Lundströmii* Cl.				r	r		
— cfr *laevis* A. Cl.				r	r		
— *minuscula* Grun.				r	r		
— *placentula* (Ehr.) Grun.				r	r		
— *pupula* Kütz.	r		r	+	+	+	++
— — v. *capitata* Hust.							
— *pseudoscutiformis* Hust.	r			+	r	r	r
— *radiosa* Kütz.				c	++	++	++
— — v. *tenella* (Bréb.) Grun.			r			r	r
— — v. *subrostrata* Cl.	r						
— *Rotaeana* (Rabh.) Grun.	r						
— *rhynchocephala* Kütz.				r	r	+	+
— *seminulum* Grun.				r	r		+
— *simplex* Krasske	r						
— subtilissima Cl.	r						r
— cfr *tridentula* Krasske	r						
— cfr *tuscula* f. *rostrata* Hust.							r
— cfr *ventralis* Krasske							r
— cfr *verecunda* Hust.				r	+		r
— *vulpina* Kütz.				r	r	r	
— *Wittrocki* v. *fennica* A. Cl.						r	
— spec. viridula var?					r		r
Neidium affine (Ehr.) Cl.				r	r	r	
— — v. *amphirynchus* (Ehr.) Cl.						r	r
— — v. *longiceps* (Greg.) Cl.	r					r	r
— *bisulcatum* (Lag.st.) Cl.				r			
— *dubium* v. *cuneata* Font.			r	r	r		
— *Hitchcockii* (Ehr.) Cl.				r	+	r	r
— *iridis* (Ehr.) Cl.				r	r	r	
— — v. *ampliata* (Ehr.) Cl.	r			+		r	
— *productum* (W. Sm.) Cl.				r	r	r	

Tabelle 8. Forts.

	Höbäcks-tjärn		Hö-bäcken	Giller-vattnet		Bruträsket	
	1950	1952	1952	1950	1952	1950	1952
Nitzschia acicularis W. Sm.						r	
— *acuta* Hantzsch					r		
— *amphibia* Grun.						r	
— *angustata* v. *acuta* Grun.	r			r		r	r
— *capitata* Östrup						r	+
— *capitellata* Hust.						r	r
— *denticula* Grun.	r			r			
— *dissipata* v. *media* (Hantzsch) Grun.				r			
— *fonticola* Grun.	r			r		r	r
— *frustulum* (Kütz.) Grun.	r			r	r		
— — v. *perminuta* Grun.	r		r	r		r	
— — v. *perpusilla* (Rabh.) Grun.				r			r
— *gracilis* Hantzsch	r			r			
— — v. *densior* A. Cl.			r	r			
— *Hantzschiana* Rabh. Grun.	r			r		r	r
— *linearis* W. Sm.	r			r			
— *Kützingiana* Hilse	r			r			
— *palea* (Kütz.) W. Sm.				r	r		
— — v. *tenuirostris* Grun.	r		r	r			
— *paleacea* Grun.				r		r	r
— *recta* Hantzsch	r			r			
— *romana* Grun.				r			
— *subtilis* Grun.	r						
— *thermalis* v. *minor* Hilse							r
Meridion circulare Ag. mit f. *constricta* (Ralfs) V. H.				r			
Pinnularia acrosphaeria Bréb.				+	+		
— *appendiculata* (Ag.) Cl.						r	
— *Brandelii* Cl.						r	
— *Braunii* (Grun.) Cl.						r	r
— — v. *amphicephala* (A. Mayer) Hust.			r	r	r		
— *Brebissonii* Kütz.	r			r			
— *brevicostata* Cl.						r	r
— — v. *leptostauron* Cl.	r			r		r	r
— *dactylus* Ehr.				r	r	+	
— *divergens* W. Sm.				r	r	+	+
— — v. *undulata* Herib. et Perag.						r	r
— *distinguenda* Cl.				r	r		
— *esox* Ehr.	r			+	r	r	r
— *gentilis* (Donk.) Cl.				++	r		
— *gibba* Ehr.	r			++	++	++	++
— *gracillima* Greg.	r					r	r
— *hemiptera* (Kütz.) Cl.				c	++	++	c
— *interrupta* W. Sm.	r			r	+	+	
— *isostauron* (Ehr.) Grun.						+	
— *karelica* Cl.				r		r	
— *lata* (Bréb.) W. Sm.				r	r		
— *laticeps* A. Cl.	r					r	
— *legumen* Ehr.	r					r	r
— *maior* (Kütz.) Cl.	r			+	+	++	++
— — v. *linearis* Cl.	r				r	r	
— — v. *transversa* A. S.				r	r		
— *macilenta* (Ehr.) Cl.						r	r
— *mesogongyla* Cl.				r	r		r
— *mesolepta* (Ehr.) W. Sm.	r			r	r	r	+
— *microstauron* (Ehr.) Cl.	r					r	r
— — v. *ambigua* Meist.				r	r		

Tabelle 8. Forts.

	Höbäcks-tjärn		Hö-bäcken	Giller-vattnet		Bruträsket	
	1950	1952	1952	1950	1952	1950	1952
— *molaris* GRUN.	r						
— *nobilis* EHR.				++		r	+
— *nodosa* EHR, f. *capitata* CL.			r	c	++	c	c
— *platycephala* (EHR.) CL.						r	r
— *stomatophora* GRUN.	r			r	r	r	r
— *streptoraphe* CL.							r
— — v. *styliformis* GRUN.						r	
— *subcapitata* GREG.	r		r			r	r
— — v. *lapponica* A. CL.	r						
— *subsolaris* GRUN.	r		r	r	r	r	+
— *viridis* (NITZSCH.) EHR.						r	r
— — v. *fallax* CL.	r			r		+	
— — v. *intermedia* CL.			r	r	r		+
— — v. *leptogongyla* (EHR.?) CL.						r	r
— — v. *sudetica* (HILSE) HUST.				r		r	+
— *undulata* GREG.	r					r	r
— spec.						r	r
Rhopalodia gibba (EHR.) O. MÜLL.	c			++	r	r	+
— *gibberula* v. *producta* A. CL.				r		r	
Stauroneis acuta W. SM.				+	+	+	
— *anceps* EHR.			r	++	++		++
— — v. *amphicephala* KÜTZ.	r					r	
— — f. *gracilis* (EHR.) CL.				+	+	+	r
— — v. *hyalina* BRUN et PERAG.				r	r	+	++
— *legumen* EHR.						r	r
— *phoenicenteron* EHR.				+	+	+	++
— *phyllodes* (EHR.) CL.						r	
— *Smithii* GRUN.	r			+	+	r	
Stenopterobia arctica A. CL.	c						
— *intermedia* (LEWIS) FRICKE				r	r	c	c
Stephanodiscus astraea (EHR.) GRUN.				r			
Surirella biseriata BRÉB.				r	+	+	+
— *elegans* EHR.	r			r	r	r	+
— *helvetica* BRUN				++			
— *lapponica* A. CL.				r	r	r	
— *linearis* W. SM.	r			r		r	+
— — v. *constricta* (EHR.) GRUN.				r	+	r	
— *Moelleriana* GRUN.							r
— *robusta* v. *nobilis* (W. SM.) A. CL.				+	r	++	c
— — v. *ovata* A. CL.				++	++	++	+
— — v. *splendida* (EHR. W. SM.) V. H.				+	++	r	++
— *simplex* v. *oblonga* A. CL.				r	r		
— *tenera* v. *nervosa* MAYER						r	
Synedra acus KÜTZ.				r			
— — v. *angustissima* GRUN.				r			
— — v. *delicatissima* (W. SM.) GRUN.				r			r
— *amphicephala* KÜTZ.							r
— *parasitica* v. *subconstricta* (GRUN.)	r			r	r	r	r
— *pulchella* (RALFS) KÜTZ. Fragm.			r	r			
— *radians* (KÜTZ.) GRUN.	r		r	+			
— *rumpens* KÜTZ.				r			
— *tenera* W. SM.			+	r			
— *ulna* v. *danica* (KÜTZ.) GRUN.	r			r	r		
— — v. *biceps* (KÜTZ.) v. SCHÖNF.				r	+		
— — v. *subaequalis* GRUN.				r			
— *Vaucheriae* KÜTZ.		rr					r
— spec.			+				

Tabelle 8. Forts.

	Höbäcks-tjärn		Hö-bäcken	Giller-vattnet		Bruträsket	
	1950	1952	1952	1950	1952	1950	1952
Tabellaria fenestrata (LYNGB.) KÜTZ.	r	r		cc	cc	r	++
— *flocculosa* (ROTH) KÜTZ.	c	r		r		+	++
Tetracyclus lacustris RALFS				++	+	+	++
— — v. *strumosa* (EHR.)						r	

erreicht. Der Sulfatwert ist auf 29 mg/l, der pH-Wert auf 5,8 gesunken, und der Alkalinitätswert ist gleich 0,16. Trotz diesen relativ guten chemischen Bedingungen sind die biologischen Verhältnisse im freien Wasser auch dieses Sees völlig verändert. Die Planktonprobe, die bei dieser Gelegenheit wie bei früheren teils in der Mitte des Sees, teils in der Strandvegetation genommen wurde, enthält nunmehr nur spärliche Reste der früher reichen Flora (Tab. 7). In der Planktonprobe aus dem offenen See sind lebend nur wenige *Tabellaria fenestrata*-Zellen, sowie eine geringere Anzahl Schalen von anderen Formen vorhanden. In der Probe aus der Strandvegetation, die mit dem Pfahlkratzer genommen wurde, ist die Kieselalgenflora reicher, aber erreicht bei weitem nicht die gleiche Individuenzahl wie früher und ist in ihrer Zusammensetzung verändert. So ist *Asterionella formosa* völlig verschwunden und *Tabellaria fenestrata* ist nicht mehr gewöhnlich wie früher. *Eunotia exigua* dagegen, die früher fehlte, zeigt sich nun als Aufwuchs auf Pflanzenresten in reichlicher Menge. In einer Probe vom Oberflächenschlamm des Bodens wurde keine Veränderung, von der man annehmen könnte, dass sie im Zusammenhang mit den Milieuverhältnissen auf Grund des Einwirkens des Grubenwassers stehen könnte, festgestellt. Die Arten- und Individuenanzahl ist ungefähr die gleiche, und es treten die gleichen Formen auf. Zwar dürften mehrere von den aufgezeichneten Formen sowohl in dieser wie in den vorhergehenden Proben aus leeren Schalenresten, die eigentlich anderen Biotopen, dem Planktonbestand des Sees und dem Aufwuchs in der Strandzone angehören, bestehen, und es ist unmöglich, in einer mit Schwefelsäure behandelten Probe zu bestimmen, welche Formen bei der Probeentnahme lebend waren. Die Tatsache, dass *Eunotia exigua,* die ausgezeichnet im Schlamm des Gillervattnet gedieh, im Bodenschlamm des Bruträsket fehlt, zeigt aber, dass die Milieu-Verhältnisse hier so normal sind, dass sich diese Alge nicht in nennenswerter Weise auf Kosten der anderen Arten entwickeln kann.

Die Entwicklung der Seen nach 1952

Schliesslich sollen einige Worte über die Entwicklung in den Bolidenseen nach 1952 gesagt werden. Am 8. August 1953 wurden erneut einige biologische Proben an den gleichen Stellen des Wasserwegs wie vorher genommen. Sie bestanden aus Bodenschlammproben vom Höbäcken, Plankton- und

Pfahlkratzerproben vom Gillervattnet und schliesslich Planktonproben vom Bruträsket. Die einzige lebende Kieselalge aus allen Proben war *Eunotia exigua,* aber diese Alge war zahlreich im Höbäcken und in dem Gillervattenbach. Aus der chemischen Untersuchung, die bei dieser Gelegenheit gemacht wurde, (Tab. 2 b, 4, 6) geht hervor, dass sich die chemischen Verhältnisse im Gillervattnet und Bruträsket verschlechtert haben, und dass selbst im Höbäcken der pH-Wert weiter gesunken ist. Aber damit scheint auch der Tiefstand des schädlichen Einwirkens des Grubenwassers erreicht zu sein. Kurz nach der letztgenannten biologischen Probeentnahme begann die zweite Etappe der Tätigkeit der Grubengesellschaft im Gillervattenweg, nämlich das Ablassen des Abwassers von dem nun fertigen Anreicherungswerk in Boliden. Dieses Abwasser enthält, wie bereits erwähnt, grosse Mengen anorganischen Schlamms, der zum grössten Teil im Höbäckstjärn und in dem diesen umgebenden eingedämmten Gelände niedergeschlagen wurde. Im übrigen hat das Anreicherungswasser einen neutralen Charakter mit einem pH-Wert von 6,5—7,0. Die fortgesetzten chemischen Untersuchungen im Gillervattenweg zeigen eine ständige Verbesserung der Wasserbeschaffenheit des Höbäckstjärn. In obenerwähnten Tabellen sind einige chemische Werte auch vom März 1954 angegeben. Auf Stat. 1, Höbäcken, und zwar vor dessen Einmündung in das Gillervattnet, ist der pH-Wert auf 6,9 gestiegen, das Wasser ist also nunmehr so gut wie neutral. Die freie Menge Sulfatjonen ist gegenüber dem vorhergehenden Jahre auf die Hälfte und die übrigen Metalljonen sind ebenso auf einen Wert gesunken, der für ein normales Pflanzen- und Tierleben unschädlich sein dürfte. Der Trübungswert dagegen ist, wie man erwarten konnte, etwas gestiegen. Wie aus der Tabelle 4 hervorgeht, hat sich die günstige Auswirkung des neuen Zuschusses von Abwasser noch nicht über das Gebiet des Höbäckstales hinaus erstreckt. Im Gillervattnet macht sich das saure und giftige Grubenwasser weiterhin in gleich hohem Grade geltend. Es wird interessant sein, bei einer kommenden biologischen Untersuchung, die wir später vornehmen zu können hoffen, festzustellen, ob die verbesserten chemischen Verhältnisse im Höbäckstjärn sich auch in den biologischen Bereich hinein zu erstrecken begonnen haben, sodass ein Teil der ursprünglichen Flora und Fauna nunmehr wieder Entwicklungsmöglichkeiten in diesem See findet. Mindestens dürften sich Voraussetzungen für eine Regenartion des Planktons finden, während die Ständer und der Boden wohl für das Pflanzen- und Tierleben durch den dort abgesetzten Anreicherungsschlamm zerstört sein dürften.

Zusammenfassung

Die Untersuchung kam zustande, nachdem Bolidens Grubenverwaltung durch Gerichtsentscheidung im Jahre 1949 die Genehmigung erhalten hatte, Abwasser der Grube und des geplanten Anreicherungswerkes in Boliden durch den sog. Gillervatten- (Gillerwasser-)weg in den Skellefte-Älv abzuleiten. Der Weg besteht aus den Seen Höbäckstjärn, Gillervattnet und Bruträsket, die miteinander teils durch natürlichen Bachabflüsse, teils durch einen neu gezogenen Graben in Verbindung stehen. Da das Grubenwasser durch Vorhandensein von freiem H_2SO_4 einen stark sauren Charakter und eine Menge gelöster, giftiger Metallsalze hat, war eine stark schädliche Einwirkung auf das Wasser in den Seen, besonders in dem erstgenannten, dem Höbäckstjärn, vorauszusehen. Es wurden daraufhin fortlaufende Wasserproben für eine chemische Untersuchung sowohl vor wie nach dem Ablassen des Wassers genommen. Das Resultat von 4 chemischen Analysen ergibt sich aus Tab. 2 a und b, 4 und 6. Weiter wurden Proben für die biologische Untersuchung bei 3 Gelegenheiten vor und nach dem Ablassen des Grubenwassers genommen. Der Teil der biologischen Untersuchung, der im obigen Aufsatz behandelt wurde, bildet eine eingehende Untersuchung der Kieselalgenflora der Seen vor dem Ablassen des Grubenwassers und der Veränderungen, die diese nach dem Einwirken des Grubenwassers während eines Jahres durchgemacht haben.

Die erste Untersuchung zeigte, dass die Seen in natürlichem Zustand einen oligo-dystrophen Charakter mit kalkarmem, wenig nahrungsreichem, klarem Wasser hatten. Sowohl das Plankton der Seen wie auch das Benthos im Strandgürtel und im obersten Schlammlager des Bodens enthielt eine mehr oder minder reiche Kieselalgenflora, bestehend aus den in den nördlichen Waldgebieten gewöhnlichen Reinwasserformen.

Nach dem Einwirken des Grubenwassers während eines Jahres ist die Kieselalgenflora im freien Wasser aller drei Seen so gut wie vollständig verschwunden. Im Höbäckstjärn und dessen Auslauf, dem Höbäcken, ist die ursprünglich lebende Flora völlig durch die Art *Eunotia exigua* (Bréb.) Grunow ersetzt, die in grosser Menge die Probe aus diesem See beherrscht. Selbst in der Strandgegend des Gillervattnet ist die *Eunotia exigua* die einzige überlebende Alge. Im Schlammlager seines Bodens kann eine verminderte Anzahl von Arten festgestellt werden, während der Bruträsket keine Veränderung in diesem Biotop zeigt. Die durch ihr Aussehen und Auftreten in diesen Seen auffallende Kieselalge *Eunotia exigua* wurde eingehend besprochen.

Schliesslich wurden der Entwicklung der Seen nach 1952 einige Worte gewidmet. Eine merkbare Veränderung konnte in der Reaktion des Wassers im Höbäckstjärn festgestellt werden, nachdem man begonnen hatte, im August 1953 Abwasser des Anreicherungswerkes in den See zu pumpen. Dieser hat nunmehr ein neutrales Wasser. Eine spätere biologische Untersuchung dürfte klarlegen, ob dieser wichtige Faktor auf die biologischen Verhältnisse in neuer Richtung eingewirkt hat.

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