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FISHERY BOARD OF SWEDEN

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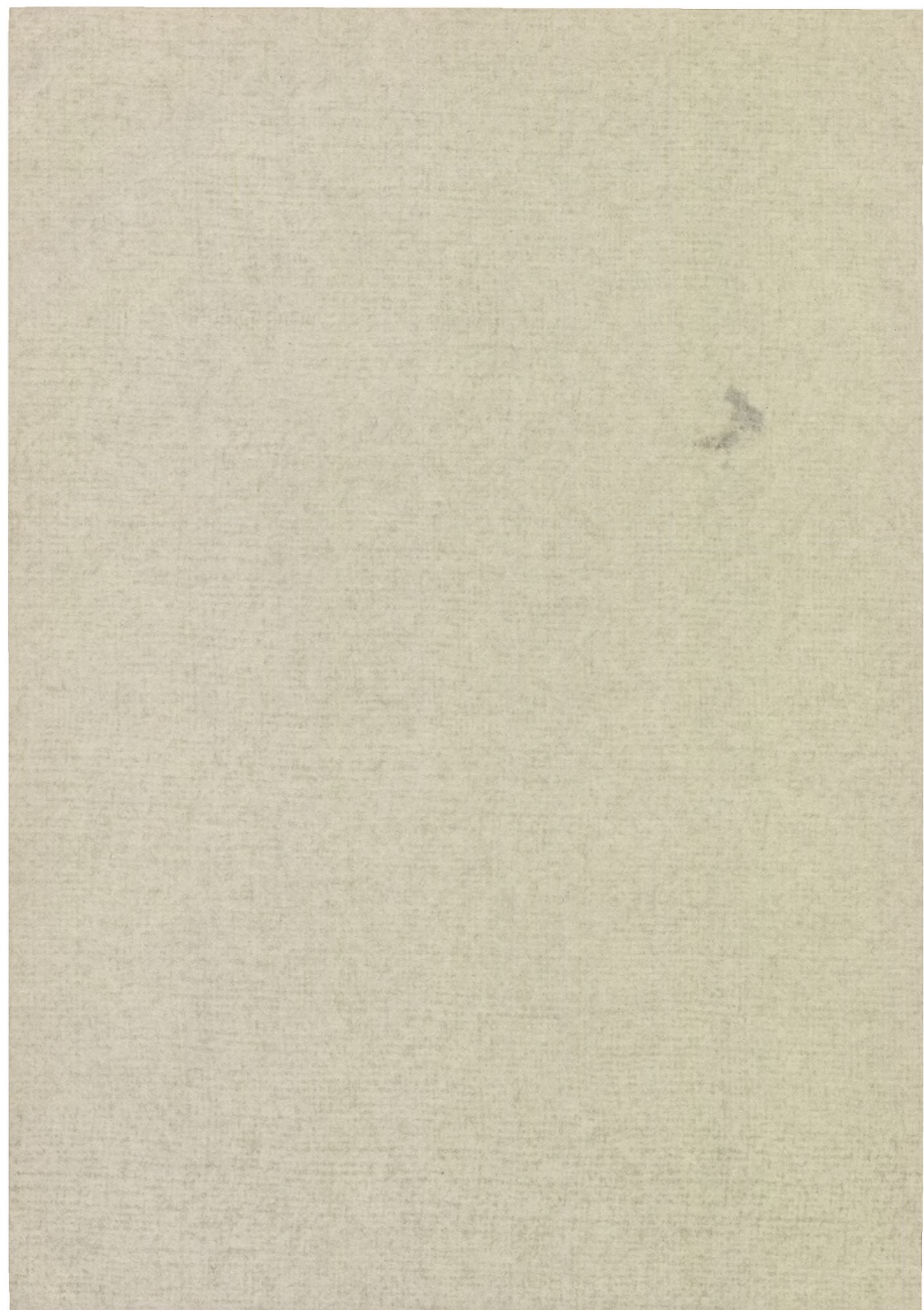
INSTITUTE OF FRESHWATER RESEARCH

DROTTNINGHOLM

Report No 40

LUND 1959

CARL BLOMS BOKTRYCKERI A.-B.



FISHERY BOARD OF SWEDEN

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Connection between Maturity, Size, and Age in Fishes
Experiments carried out at the Kälärne Fishery Research Station

By GUNNAR ALM

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I. Introduction

In all investigations dealing with fish populations and their rational exploitation a knowledge of the growth and age of the individuals and of their sexual maturity (maturation or first time spawning) is of great importance. The literature on fishery also contains numerous informations about age and size at maturity in different species and forms, and also in different populations of the same species and form. There exist also many informations about poorer growth and increased mortality in connection with maturity and spawning, and about differences in this respect between males and females. In several cases, however, the mentioned informations contradict each other and the problem is complicated by the known lability of growth in fishes.

It is also connected with great difficulties to obtain reliable results in these respects, when carrying on experiments and investigations in the field. In ponds on the other hand it should be possible to study the conditions in a more reliable way. There yearly investigations during spawning time can serve to control in different experiments maturity, growth, and mortality by the marking of groups which are kept separate. It is also possible to decide, whether or not spawning takes place every year, and to form a certain idea about the age of different species of fish.

For these reasons the work at the Kålarne Fishery Research Station has since a long time been directed towards these problems, and a great number of experiments has been carried out, the results of which will be submitted in the following. Also certain material from a number of other experiments, carried out for other purposes, has been included, often only for one or some years. The main questions to be answered were the following. Which is the connection between maturity and the size (growth rate) and age of the fish, and with the sex? Does this connection exhibit differences, when different populations of one and the same species of fish are examined? Are maturity and spawning accompanied by more obvious changes in the continued growth and the mortality?

Against these experiments the objection can of course be raised that conditions in a pond and in nature are not the same. The close agreement of the results of different experiments and with different species of fish, when it comes to the here mentioned questions, and which will be demonstrated in the following indicates nevertheless a considerable regularity. This ought then to be valid irrespective of the habitat of the fish.

II. Material and Methods

Kålarne Fishery Research Station is situated in the wooded parts of central Sweden at the latitude of 63°N . and about 100 kms. from the coast, and at an altitude of 300 ms. above sea level. The annual mean temperature at Östersund is $+2.4^{\circ}\text{C}$., that for July $+14.2^{\circ}\text{C}$. In the neighbourhood exists

a great number of small and medium size lakes, and at the station itself a number of experimental ponds of different types is found. Most of the ponds have a size of 7—8×70—90 ms. and a depth of about 0.5—1.0 m. Others with a size of from 300 to 1000 sq.ms. are shallower. The water consumption is 200—250 l/min. for the deeper ponds, and about 100 l/min. for the others. The water for the ponds is taken from the brook discharging the oligotrophic Lake Ansjön. It is clear with a pH of about 7.0 and a highest temperature of 22—23°C. In all ponds there exists at the borders and partly also in the pond itself a sparse vegetation of species of the genera *Equisetum*, *Carex*, *Myriophyllum*, *Potamogeton*, *Utricularia*, *Characeae*, etc. There also exists a rich fauna composed of species typical for biotopes of this kind, especially larvae of libellulids, ephemerides and trichopteres and species of *Limnaea* being common. From a certain point of view the ponds can thus be compared with parts of lakes.

In order to ameliorate the supply of food for the larger fish feeding has been carried out, mainly with finely cut roach and perch caught in nearby lakes, occasionally also with liver. The feeding began in spring as soon as the fish showed willingness to eat, and continued towards autumn as long as the fish exhibited appetite.

The experiments dealt mainly with two forms of Brown Trout, one a small river trout, *Salmo trutta fario* L. from Kälärne, the other a big trout from Lake Vättern, *Salmo trutta ferox* or *lacustris* L. Further on the Perch, *Perca fluviatilis* L. has been the object of a very great number of experiments. Apart from these the experiments dealt, although to a smaller extent, with other forms of trout as well as with Grayling, *Thymallus thymallus* L., Brook Trout, *Salmo fontinalis* L., Rainbow Trout, *Salmo irideus* Gibb., Whitefish, *Coregonus* sp., and finally with hybrids of different races of trout, of Char, *Salvelinus salvelinus* L.×Brook Trout and of Salmon, *Salmo salar* L.×Sea Trout, *Salmo trutta trutta* L. Also Roach, *Leuciscus rutilus* L. has been experimented with. To rear the Char in these ponds proved impossible.

The roe used for providing fry for the different experiments always was a mixture of roe from several females, fertilized by milt from several males. This was done in order to approach conditions in a natural population. The roe has been obtained from fishes at Kälärne as well as at other hatcheries, and from fish in natural lakes.

The number of individuals used in the different experiments varied in a high degree, making it possible to obtain differently growing populations. This was achieved also by simultaneously keeping in the ponds other species of fish in different number, but of roughly the same size as the experimental fishes. The intention thus was to imitate the conditions in natural waters with their sometimes rich, sometimes poor populations, and in this connection to study maturity. In several experiments a separation of larger and smaller individuals has been carried at a certain age. These were

then either left in the same pond or were distributed into different ponds in order to avoid competition. Sometimes also experiments of the same age have been lumped together, especially, where the distribution of sizes and the sexual percentages were similar. Occasionally this has been done also on account of wanting space (lack of ponds).

On all rearing in ponds experience has shown the real growth of the fish to take place in the summer, even when feeding is carried out. The same applies on the whole also to natural waters. Already earlier (ALM 1939, 1946) I have pointed out that this is the case at Kälärne, and I have exemplified the fact by means of a large numerical material. Here the actual period of growth thus comprises the time from the middle or end of May, when the ice breaks up, to the beginning of October. At these times, which on the whole correspond also to the usual spawning time of the fishes used in the experiments, the ponds were drained. On this occasion all fish with the exception of the yearlings have been examined as to number, size, sexual maturity, spawning, etc. Examination of numerous specimens in different experimental series has shown maturity of yearlings to occur only in certain populations of big-sized perch.

In the experiments which comprised a fairly large number of individuals every maturity group from a special year-class, i.e. the specimens of each sex taking part in the spawning for the first time, have been separated by marking (cutting of 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 ripeness and spawning take place annually or only with certain intervals. As far as could be observed this method of marking has not had any injurious effect.

All cutting of fins has, however, to be done very meticulously so as to prevent the fin from growing out again. It is easily carried out e.g. in perch, but more difficult in salmonids, where also the fins seem to have a greater ability of regrowth. On this account it is possible that in certain instances one or the other individual was counted as mature for the first time in spite of the fact that it had been mature, and had been marked already in the preceding year. In certain experiments the different groups of sexual maturity have not always been kept apart, but only the number of spawning specimens and their size have been taken down.

When rendering an account of the number of fish examined, it is sometimes found that at a later examination the number exceeds that found at an earlier one. This derives from the difficulty in getting all the fish out of the pond. Some specimens could be left in the pond, and be included in the next count.

On account of the mentioned connection between growth and the summer period age and size were designated by the terms 2, 3, 4 years, etc., irrespective of whether the fish were examined at the end of a preceding or the

beginning of an approaching period of growth. Thus, if a trout is examined during the spawning time in autumn, and then ought actually to be called of two or three, etc. summers, it is spoken of as of two or three years. A perch of two years on the other hand is examined during its spawning time in spring, and is thus fully 2 years old. For the salmonids consequently somewhat low values regarding the length have been obtained, since after all a certain growth takes place during the winter. This difference is, however, without significance in this connection. The length has always been measured from the tip of the nose to the tip of the expanded caudal fin, and has been adjusted to the nearest whole centimetre. As a rule the number of individuals in a certain experiment has been so great that the average length at different ages could be taken as a relatively safe figure for the size. In cases, where the spreading and at the same time the losses have been great the loss of some particularly great or small individuals could, however, produce a change in the figure for the average length.

The term *maturity* has been used in order to designate the change from the immature or juvenile fish into the sexually mature stage. Maturity terminates in first-time spawning. It consequently takes place only once in the life of each fish. All fishes which once have reached maturity are called *mature*. The term *ripeness* is used to designate the full development of roe and milt, and the release of spawning, irrespective of, whether we have to do with an earlier or a later spawning of the individual. Ripeness therefore recurs in most species of fishes several times during the lifetime of the individual. Thus a fish can be mature without being ripe, i.e. if it has attained maturity and ripeness on an earlier occasion, but later omits spawning in one year.

As far as maturity and ripeness are concerned it has in general, at least with the males, been fairly easy to decide, whether a fish was juvenile or mature. With the females certain difficulties could sometimes arise. Yet by the killing and examination of some specimens of different types it has been possible to obtain criteria for deciding which of the remaining specimens were mature or not. In several instances a greater number or all specimens in a certain experiment have been preserved, and dissected for the examination of the maturity and the development of testicles and ovaries. Then it has occasionally been found that some isolated individuals had been mature, although this had not been observed in the examination of the fish in living condition that often preceded preservation. An account of the circumstances mentioned the reported number of mature specimens can, in some few cases, have turned out somewhat lower than the actual figure. In isolated cases weather conditions prevented the tapping of the ponds at the time fitting in with the spawning time of the fish. No observations on maturity and spawning were then possible, and a gap has resulted in the corresponding experimental series.

Table 1. *The material.*

Age	Small river trout	Big trout, Lake Vättern	Big trout from Swizerl.	Small river trout × big trout, Lake Vättern	Big trout, Lake Ansjön × big trout, Lake Vättern	Salmon × seatrout	Seatrout × salmon	Brooktrout	Char × brooktrout	(Char × brooktrout) × brooktrout	Rainbowtrout	Grayling	Whitefish	Perch	Roach	Age
1	—	—	—	—	—	—	—	—	—	—	—	—	—	12,427	500	1
2	2,924	2,040	251	155	670	—	—	251	867	614	120	800	532	3,281	185	2
3	1,833	1,320	234	122	525	440	436	153	643	285	101	789	418	2,144	51	3
4	1,497	1,079	143	105	—	293	429	172	614	222	90	439	388	1,728	12	4
5	1,147	921	131	63	—	216	388	108	467	146	—	352	276	1,000	12	5
6	801	721	—	58	—	55	50	—	240	83	57	119	104	742	11	6
7	615	532	—	—	—	—	—	—	170	—	—	—	76	571	—	7
8	374	387	—	—	—	—	—	—	—	—	—	—	—	437	—	8
9	342	283	—	—	—	—	—	—	—	—	—	—	—	408	—	9
10	250	235	—	—	—	—	—	—	—	—	—	—	—	86	—	10
11 <	87	—	—	—	—	—	—	—	—	—	—	—	—	201	—	11 <
Total	9,870	7,518	759	503	1,195	1,004	1,303	684	3,001	1,350	368	2,499	1,744	23,025	771	

Losses by predators (of the same or of other species) in the ponds have probably not been especially great. Even where the differences in size were striking in the same pond, numerous smaller specimens were found, and had thus not been eaten by the larger ones to any greater extent. The losses by diseases and those probably due to birds and mink as well as those in connection with the draining of the ponds and the handling of the fish have, however, occasionally been fairly great. Thus at the annual examination frequently some specimens have been removed for a detailed investigation and control of maturity or for certain special experiments. It could, furthermore, not be prevented that some specimens died in connection with the measuring of the length, the marking, and the examination of maturity. Also the weather conditions at the time of the taking-up of the fish have influenced mortality. The above-mentioned reasons accounted for a higher mortality in warm weather than in cool and rainy weather. In the case of the salmonids, finally, the mature specimens have often been detained in tanks for the artificial fertilization of the roe, and also on these occasions a number of specimens usually died.

The nearby Table 1 provides a review of the entire number of examined specimens, distributed over species and age groups. In this connection it has to be remembered that it is obviously the same specimens which to a large extent reappear year after year with increasing age. It has to be pointed out that the figures reproduced in this Table do not supply any idea about mortality or other losses, quite a number of experiments having been terminated at a certain age, either because the number of specimens was too small or

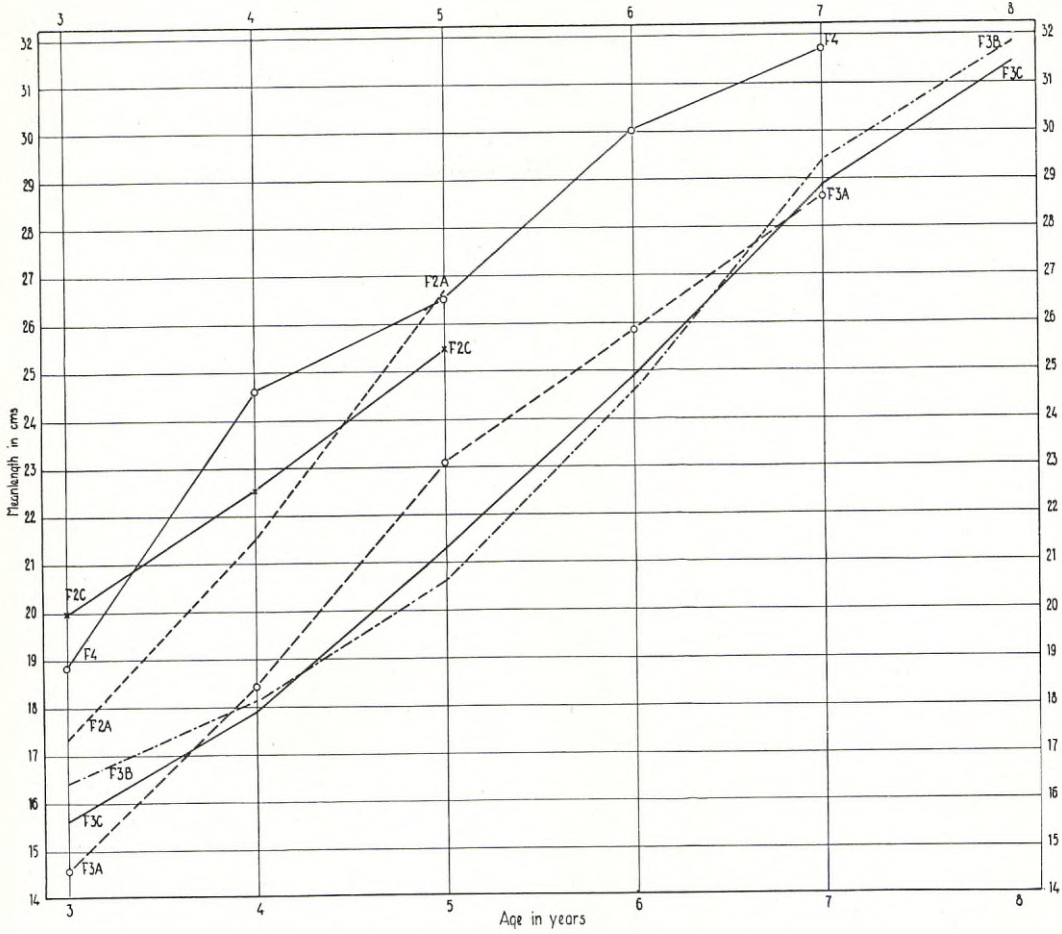


Fig. 1. Small river trout. Rate of growth in the most important experiments.

because the fishes in question had been transferred into natural waters. Other experiments again have been started at a higher age.

For every form or species the results of the experiments have been summarized in synoptic tables in the text, but especially in a great number of diagrams which in many cases are more telling than the text. In all experiments was the initial problem to obtain an idea about the age and the size of the individuals at which, as well in the same experiments as in experiments with different growth, maturity is reached. This becomes evident from the percentage of mature males and females with regard to the total number of specimens of the same age in every experiment. Since both earlier and later investigations showed the initial ratio of the sexes to be roughly 1 : 1, the figure 25 % males e.g., indicates that about one half of all males in the experiment are mature. Consequently the figure 50 % males means that

probably all males have reached maturity. Disarrangements in the sex ratio obviously sometimes occur so that in a certain experiment 60 % males and 40 % females are found at full maturity or perhaps on the contrary a greater number of females. For every species or form the different experiments have been assembled in groups of the same age arranged in order from the smallest to the greatest average length within each experiment. Here the average length has been calculated from all fishes of the same age. In other tables and diagrams the material has been split into different maturity groups within every experiment.

Certain experiments have been carried out not only in the ponds, but also in lakes empty of fish within the region. Trial fishing during autumn has in this way supplied additional valuable material for judging age and size at maturity.

III. Results

1. Small river trout from Kälärne

Table 2 gives the results of the experiments with this form of trout. With the aim of supplying a clearer view of the growth in different experiments the experiments comprising more than one year have been represented in Fig. 1 by growth curves based upon the values for the average length in Table 2. From this it can be seen that it has been possible in certain experiments to obtain almost all the time a good (F2A, F2C, and F4) or a poor (F3A, F3B, and F3C) growth, corresponding to year groups with fast and slow growth. In other experiments the growth has been good in some years and poor in others with the result that the growth curves occasionally intersect each other.

The length of mature and immature specimens of the same age within a certain experiment

Table 2 contains for every experiment and for every age figures for the average length of mature males and females and of immature specimens, each by itself. These figures of which a graphic representation for the first years of maturity is given in Fig. 2 show that in almost all experiments and for every age the average length of the mature specimens exceeded that of immature specimens of the same age. This fact must be explained by the assumption that the faster growing specimens reach maturity earlier than specimens with a slower growth. We notice furthermore that at the age of 4 years, when the females started to reach maturity, their average length mostly exceeded that of the males. During the 5th year a reversal takes, however, place in this respect, and from then onwards the length of the mature males was almost without exception greater — occasionally by several centimetres — than that of the females. This evidently implies that in this form

Table 2. *Small river trout*. Length and maturity at different ages.

Exp.	Age	Total num.	Percentage of number			Mean length in cms.			Year of exam.	
			Mature		Im-mat.	Total	Mature			Im-mat.
			♂	♀			♂	♀		
F3C	2	510	—	—	100	11.0	—	—	11.0	1949
F1C	2	415	—	—	100	ab. 11.0	—	—	ab. 11.0	1936
F2B+C	2	236	—	—	100	ab. 11.5	—	—	ab. 11.5	1941
F4	2	305	—	—	100	12.2	—	—	12.2	1952
F1A+B	2	543	—	—	100	ab. 12.0	—	—	ab. 12.0	1935
F2A	2	220	—	—	100	12.3	—	—	12.3	1939
F3A	2	350	—	—	100	12.7	—	—	12.7	1945
F3B	2	345	—	—	100	13.2	—	—	13.2	1948
F1C	3	48	—	—	100	13.4	—	—	13.4	1937
F1A	3	135	—	—	100	14.5	—	—	14.5	1936
F3A	3	199	0.5	—	99.5	14.6	16.0	—	14.6	1946
F3C	3	439	3	—	96	15.6	20.4	—	15.4	1950
F2B	3	88	16	—	84	16.0	17.8	—	15.7	1942
F3B	3	280	4	—	96	16.4	20.5	—	15.9	1949
F1B	3	55	11	—	89	17.1	?	—	?	1936
F2A	3	173	10	1	89	17.3	?	?	?	1940
F4A	3	243	13	1	86	18.8	21.5	24.5	18.5	1953
F1D	3	38	35	3	62	19.3	20.7	20.0	18.6	1937
F2C	3	135	37	1	62	19.9	20.2	23.0	19.2	1942
F3C	4	384	17	4	79	17.9	22.2	24.3	15.6	1951
F3B	4	273	19	1	80	18.1	20.1	24.0	17.5	1950
F3A	4	181	24	3	73	18.4	20.7	22.4	17.5	1947
F1A	4	73	27	3	70	18.6	?	?	?	1937
F1C+D	4	51	29	12	59	19.7	20.3	21.8	19.0	1938
F1B	4	24	38	13	49	20.4	21.4	23.0	19.0	1937
F2B	4	59	44	24	32	21.3	20.7	22.3	19.5	1943
F2A	4	142	48	30	22	21.5	?	?	?	1941
F2C	4	127	47	40	13	22.5	22.9	22.6	21.0	1943
F4A	4	183	46	37	17	24.6	24.8	25.5	21.8	1954
F3B	5	243	50	21	29	20.6	21.1	20.6	19.7	1951
F3C	5	333	31	22	47	21.3	25.2	24.7	17.4	1952
F3A	5	144	60	33	7	23.1	23.8	22.4	22.1	1948
F2C	5	87	52	36	12	25.4	25.7	25.1	24.6	1944
F1A+B	5	59	46	49	5	25.8	26.9	25.1	25.1	1938
F4	5	105	50	47	3	26.5	27.8	25.8	22.7	1955
F2A	5	133	53	44	3	26.6	27.3	25.6	23.3	1943
F2B	5	43	58	16	26	27.3	27.9	25.7	27.0	1944
F3B	6	194	54	46	0	24.6	25.8	23.6	—	1952
F3C	6	295	46	39	15	24.9	27.2	25.1	19.2	1953
F3A	6	123	62	36	2	25.9	27.1	25.9	25.3	1949
F2B+C	6	113	48	50	2	28.3	28.6	28.1	22.5	1945
F4	6	76	46	53	1	30.0	31.9	28.5	25.0	1956
F3A	7	112	61	38	1	28.7	30.4	26.5	28.0	1950
F3C	7	252	51	46	3	28.8	30.3	27.6	23.3	1954
F3B	7	189	54	46	0	29.3	30.6	27.9	—	1953
F4	7	62	50	50	0	31.7	35.2	28.1	—	1957
F3C	8	229	53	46	1	31.4	32.5	29.4	29.0	1955
F3B	8	145	54	46	0	31.8	33.3	29.9	—	1954
F3B	9	128	55	45	0	32.2	33.8	30.0	—	1955
F3C	9	214	52	48	0	32.6	34.6	30.5	—	1956
F3C	10	145	47	53	0	33.5	36.2	31.2	—	1957
F3B	10	105	55	45	0	34.1	36.1	31.6	—	1956
F3B	11	87	53	47	0	35.5	37.9	33.0	—	1957

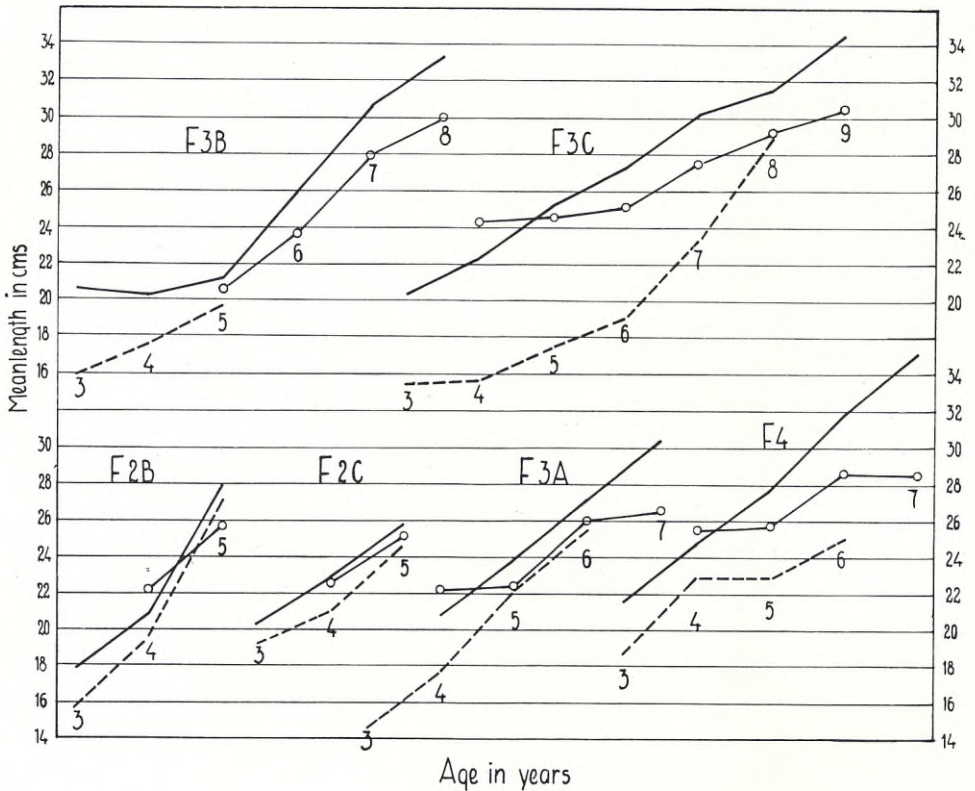


Fig. 2. Small river trout. Mean length of mature males and females and of immature specimens. ———=mature ♂; ○—○=mature ♀; - - - - =immature specimens. The figures at the growth-curves indicate the age.

of trout the females grow more slowly than the males, at least during the later part of their lives. This applies probably also during the earlier years. Table 2 shows the number of females that were mature at the age of 4 years to have been relatively small. If it is true that the specimens with the fastest growth are the first to reach maturity, it is only natural that the average length of a small number of females should exceed that of a greater number of mature males of the same age. This difference is levelled out, when with increasing age more females become mature, and on the maturity of the majority of the females the above-mentioned real difference in size between the sexes becomes evident as can clearly be seen in Fig. 3.

These relations between maturity, and size and sex are more clearly shown in Figs 4—7. These exhibit for each length group and with rising age the number of mature males and females and that of immature specimens. For economy of space only two experiments with good and two with poor growth have been included here. The diagrams exhibit more or less typical

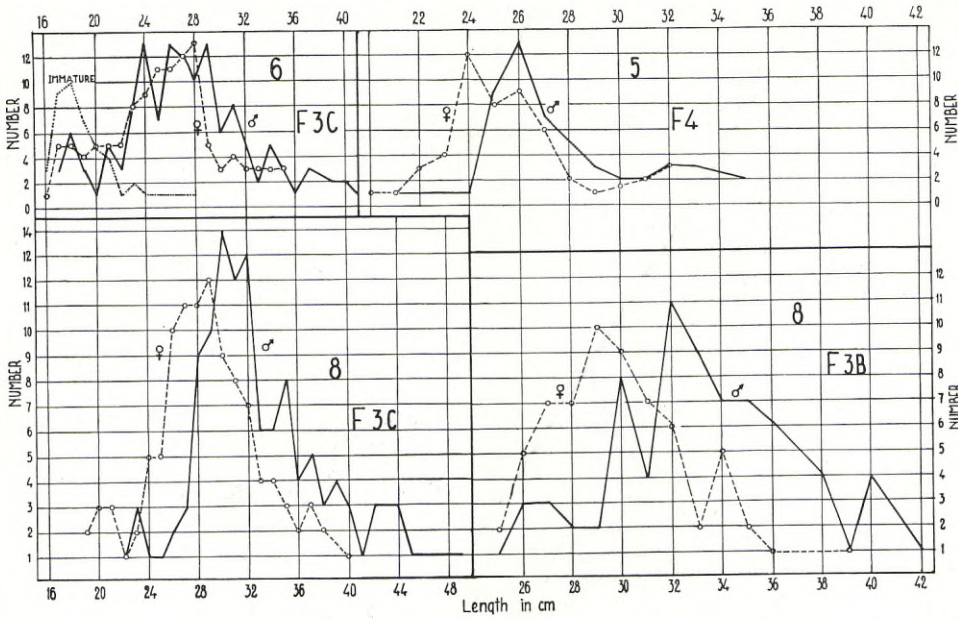


Fig. 3. Small river trout. Size distribution of mature males and females and of immature specimens. The figures in the experiments indicate the age.

binominal size curves. The amplitude of variations varies in different experiments, and is rather wide. It often increases with growing age. It is, however, very evident that for each age mature specimens were found mainly within the groups of greater length. Among these mature specimens the males were furthermore more common within the larger length groups, while the females were commoner in the shorter groups. Often these differences are very striking for each age group and for each experiment, and the same applies for the remaining experimental results, which have not been graphically represented, although certain exceptions do occur. The uniform tendency of the figures for the average length given in Table 2 is thus in general not due to some isolated particularly big or particularly small specimens. In every one of the three groups the size exhibits a universal difference.

In order further to examine the connection between size and maturity two experiments with separation into different size groups were carried out. In one of them (Fig. 8) a number of 3-year-old specimens were distributed into a) 72 smaller specimens, 14—17 cms., average length 16.2 cms., and b) 63 larger specimens, 18—27 cms., average length 19.5 cms. They were kept in the same pond, but distinguished by the cutting of fins. At this time 16 males and 1 female were mature in the larger group, none in the smaller group. After one year the size curves coincided in part, but the average lengths

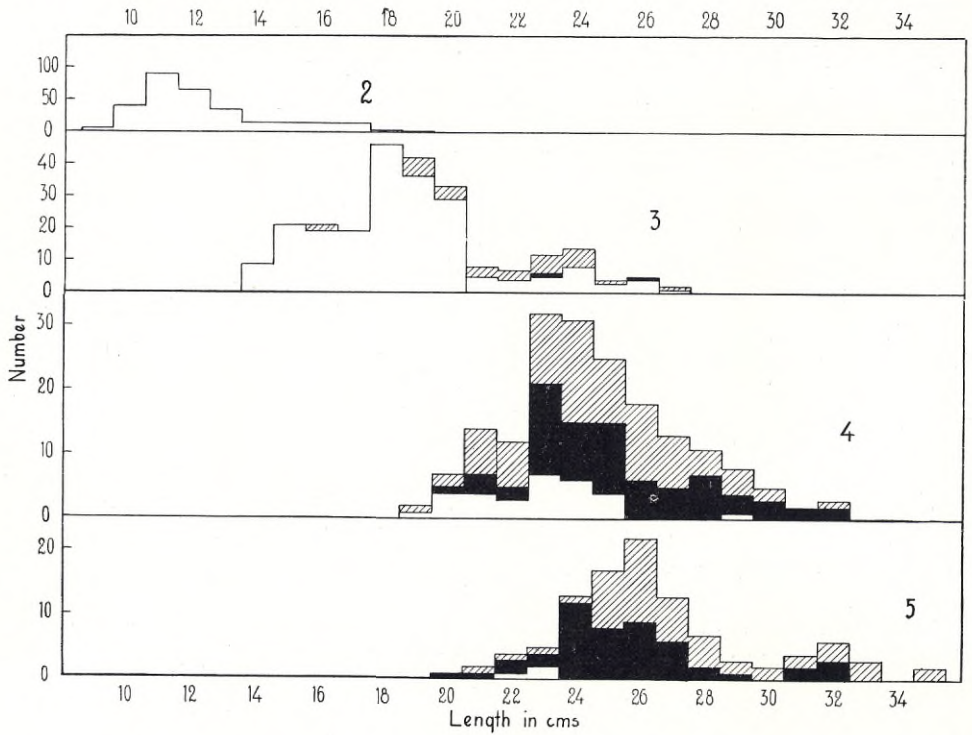


Fig. 4.

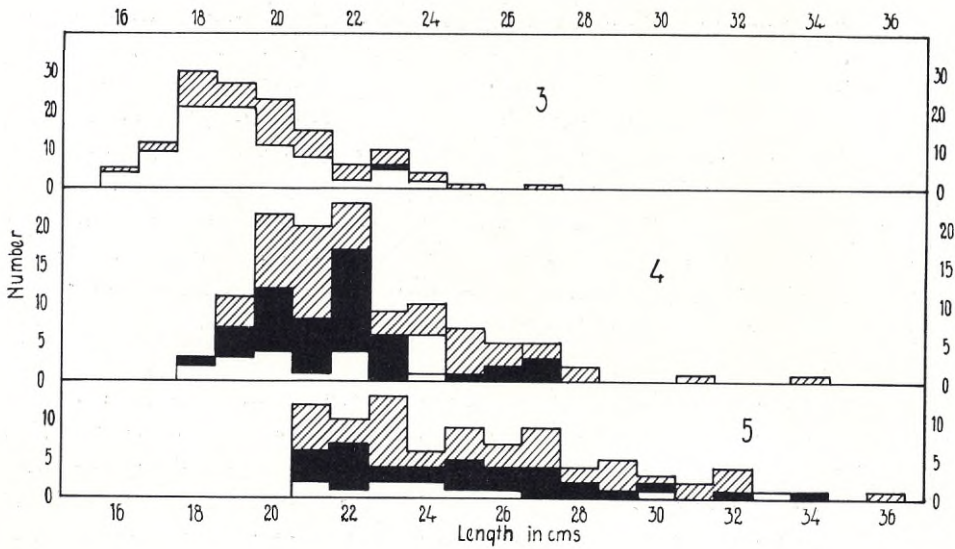


Fig. 5.

Figs. 4—7. Small river trout. Number of mature males and females and of immature specimens in different size groups at different ages in two fast growing and two slow growing experiments. Fig. 4, exp. F4. Fig. 5, exp. F2C. Fig. 6, exp. F3B. Fig. 7, exp. F3C.

▨ = ♂, ■ = ♀, □ = immature specimens.

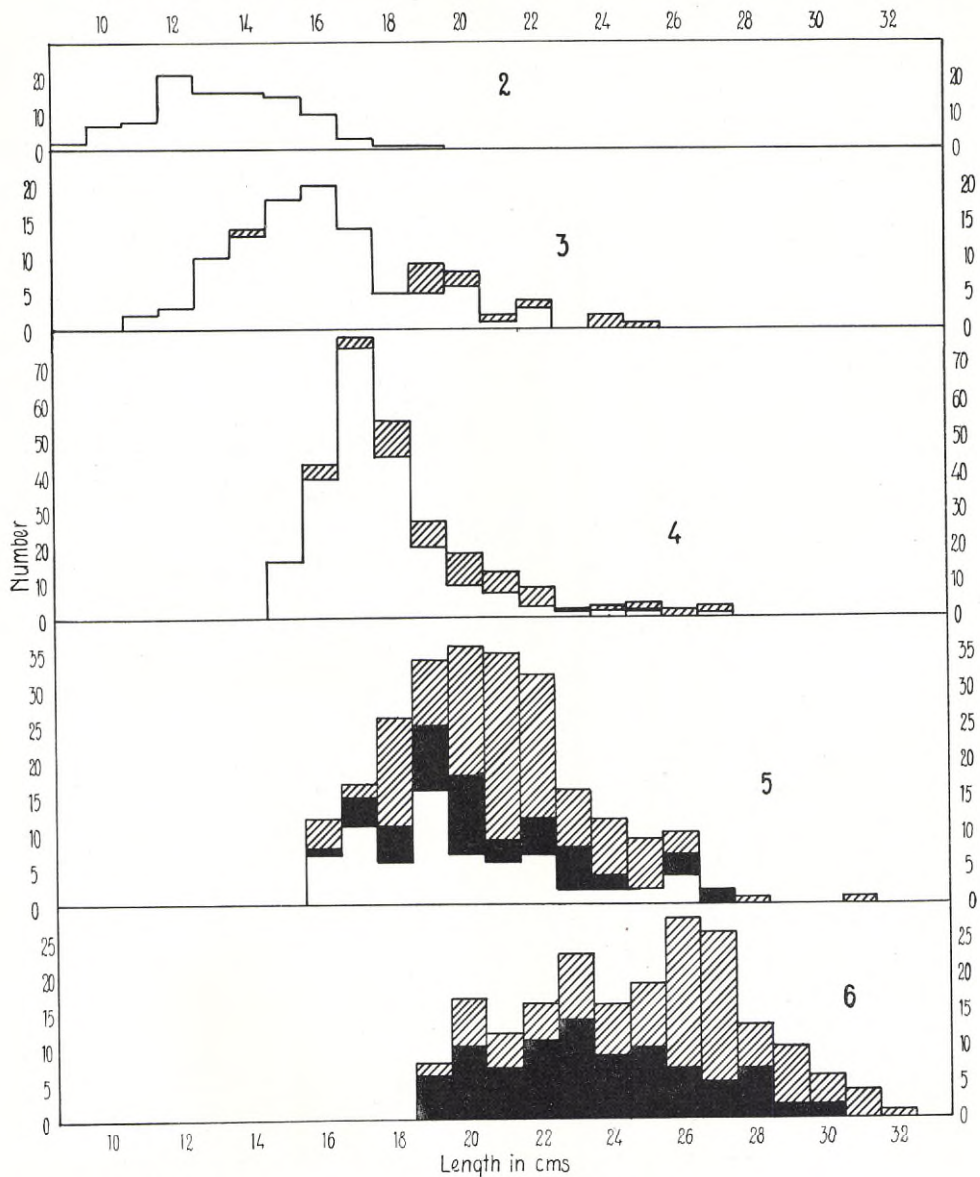


Fig. 6.

were nevertheless different, viz. 19.9 cms. in group a) and 23.4 cms. in group b). Group a) now contained 46 % males and 15 % females, group b) on the other hand 53 % males and 39 % females. Thus the maturity percentage was considerably higher among the larger specimens in group b), especially for the females. The length of the mature specimens has not been measured.

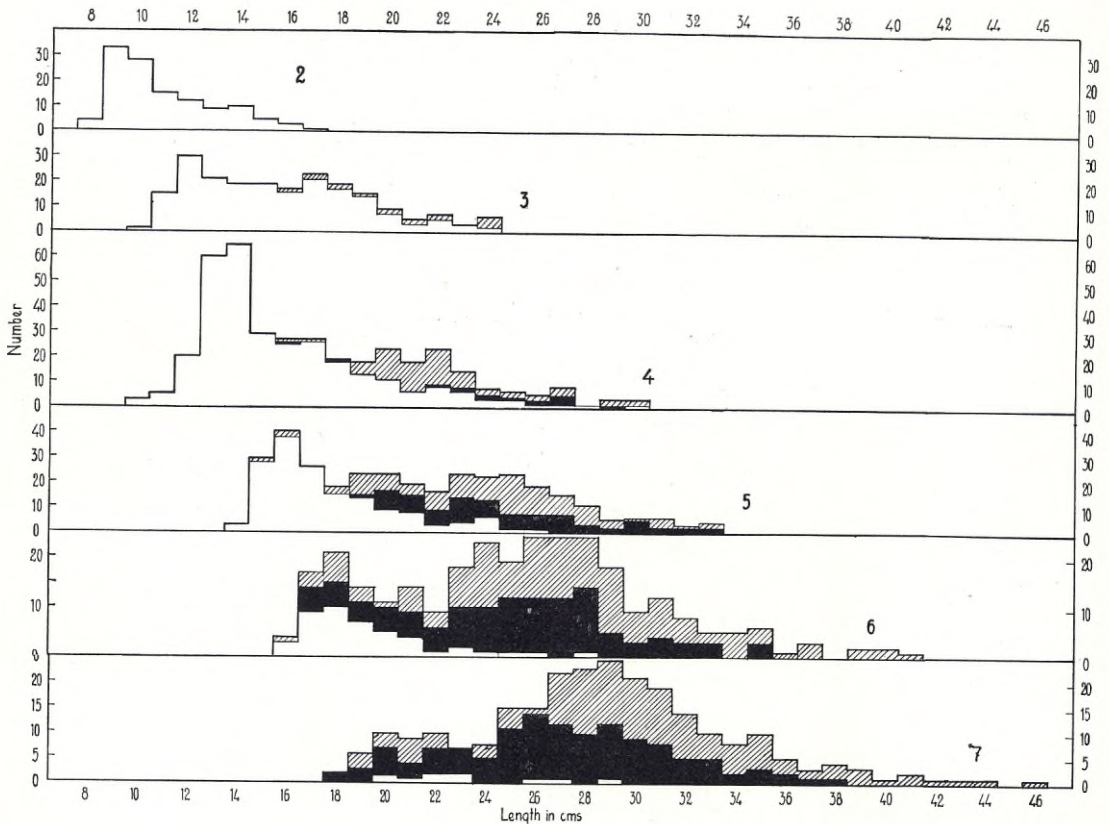


Fig. 7.

The other experiment entered into experiment F4. Also here a separation like that in the just mentioned experiment was carried out. All specimens of 3 years' age were distributed into a) 191 specimens of 14—20 cms. and b) 52 specimens of 21—27 cms. These were, however, placed into different ponds under conditions which should have given the small-sized group good opportunities of reducing the lead in size of the large-sized group. At the age of 4 years there remained, however, a distinct difference in average length; 23.8 cms. in group a) against 26.7 cms. in group b). The length varied between 19—32 and 23—32 cms., respectively. Thus the largest specimens were of the same size in either group. The percentage of immature specimens was 18 in group a), but only 8 in the large-sized group b). In the continuation as experiment F4 the two groups were again joined.

The number of mature specimens of the same age in experiments with better and poorer growth (=year classes with different growth)

Fig. 9 exhibits for all experiments the relation between the percentages of mature specimens, males and females being treated separately, and the

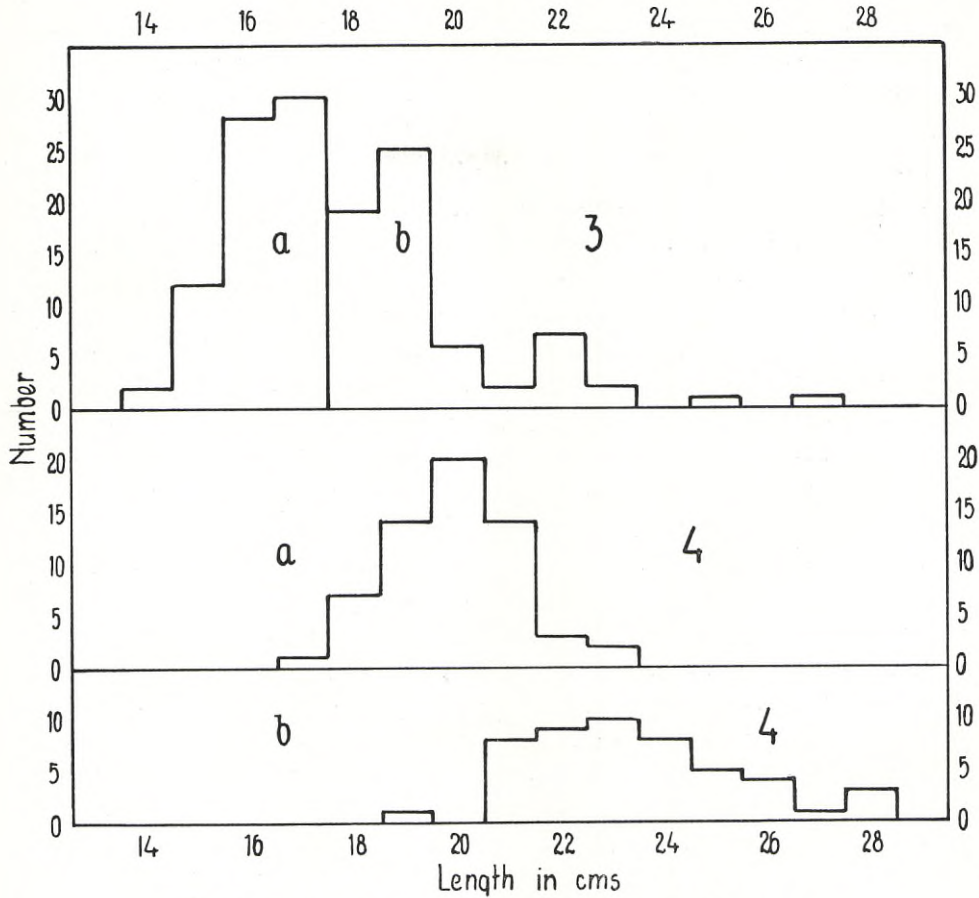


Fig. 8. Small river trout. Separation into two length groups.

average lengths of all specimens in the experiments concerned. Everything is arranged according to different age classes. The beginning was made with the 3-year-olds, since at the age of two years mature males have been encountered only in isolated cases, whereas mature females have never been found among them. This diagram is supplemented by Fig. 10 which shows the percentages of mature males and females at the age of 3 and 4 years in all experiments entered into Table 2, the arrangement being from the smallest to the greatest average length.

A closer study of these two diagrams and of Table 2 shows the way in which the number of mature specimens depends on both age and size. Thus the figure for the percentage of mature specimens grows, with rising age, as is quite natural. But in experiments with identical ages it grows on the whole also with increasing average size. This connection with size has the result that in experiments with well-grown and large fish of 3 years the

percentage of mature specimens is equal to and sometimes even larger than in experiments with slowly growing fish of 4 years. And the same remark applies to comparisons between experiments with big-sized 4-year-old and small-sized 5-year-old fishes.

With regard to the age for maturity it has already been mentioned that a few males had become mature already at the age of 2 years. Generally, however, maturity starts to develop in males only during the third year, and to a larger extent only in case the growth has been relatively good. In certain experiments with poor growth no or only a few males of 3 years were mature. At the age of 4 years nearly all males were mature in the former experiments, but only $\frac{1}{4}$ — $\frac{1}{3}$ of all specimens in the later experiments. This is particularly obvious from Fig. 10. At the age of 5 years generally about 50 % of all specimens were mature males. This implies that now practically all males have reached maturity, also in the experiments with poor growth. Only in experiment F3C several males were still immature at this age.

Among the females some isolated specimens became exceptionally mature at the age of 3 years, but this happened only in the experiments with the fastest growth. The same applies to the experiments with slowly growing females of 4 years. At this age the maturity increased, however, quickly with increasing average length, as is clearly visible in the diagrams. This was the case also with the 5-year-old fishes. In experiments with especially poor growth a large number of females was still immature there. In the more fast-growing experiments on the other hand the percentage of mature females was so high that almost all females could be assumed now to have reached maturity. Experiment F2B with only 16 % of mature females constituted an exception. In this case it is, however, probable that some specimens counted as immature were in reality mature females, though this fact had not been established. This assumption is supported by the fact that, contrary to what is otherwise the case, the average length of the former was greater than that of the latter. In experiment F3C and to an even greater extent in experiment F3A a rather small number of mature females were found at the age of 6 years. In the latter case this derives, however, from the percentage of the males being here unusually high, 62 % of the total, whereas the number of immature specimens, certainly females, amounted to only 2 per cent.

The above-mentioned Figs. 4—7 show more clearly than Figs. 9 and 10 the different age at which maturity is reached in experiments with different rate of growth. While in the experiments F4 and F2C (Figs. 4 and 5) the majority of the 4-year-olds was mature, the experiments F3B and F3C (Figs. 6 and 7) contained only a smaller number of mature individuals. Also among the 5-year-olds there occurred in the later experiments a great number of immature specimens, in either case mainly among the groups of small size.

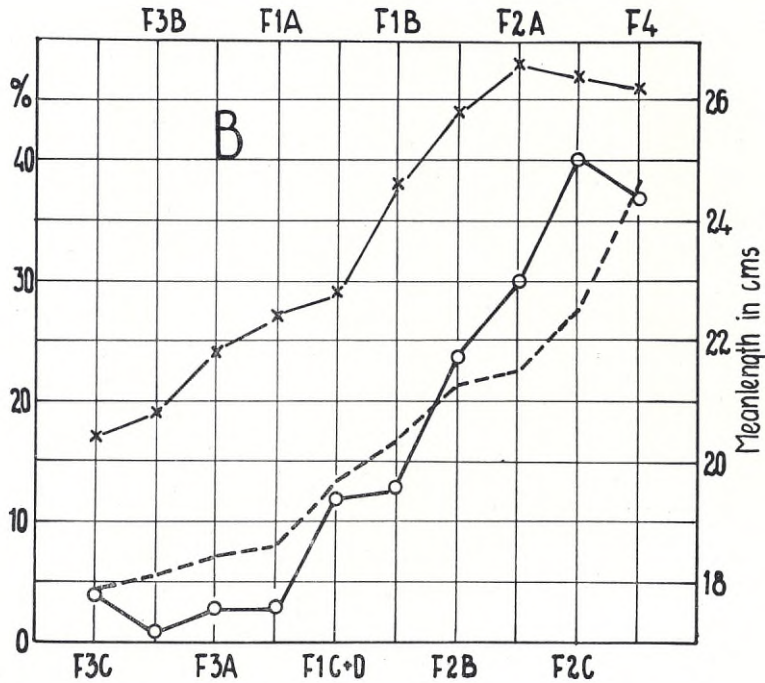
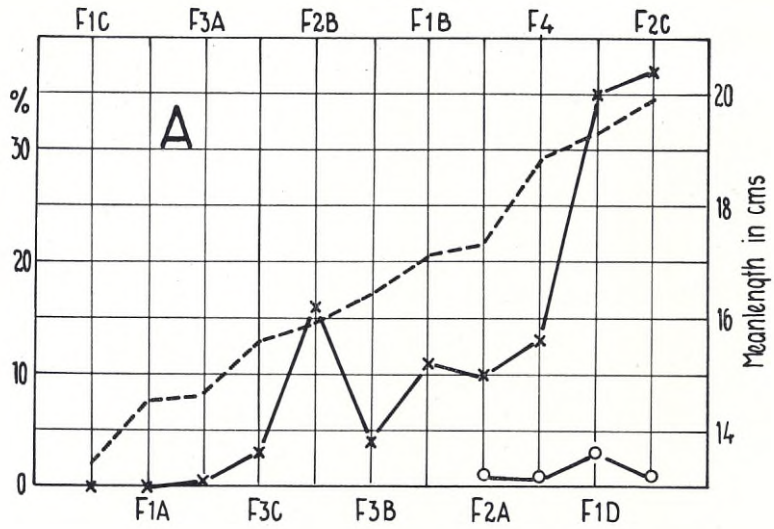


Fig. 10. Small river trout. Percentage of mature males and females in experiments with A) 3- and B) 4-years old specimens. $\times-\times-\times = \text{♂}$, $\circ-\circ-\circ = \text{♀}$, -----=mean length in the experiments.

Table 3. *Small river trout*. Number and percentages of mature males and females at different ages.

Age	Mature				Immature	
	♂		♀		Number	%
	Number	%	Number	%		
3	163	8.9	5	0.3	1,665	90.8
4	443	29.7	208	13.9	846	56.4
5	577	50.2	347	30.3	223	19.5
6	404	50.0	346	43.2	51	6.8
7	328	53.3	276	44.9	11	1.8
8	199	53.2	172	46.0	3	0.8
9	183	53.5	159	46.5	—	—
10	126	50.4	124	49.6	—	—
11	46	52.9	41	47.1	—	—

In the fast-growing experiments on the other hand only isolated specimens, mostly of the groups with the smallest size, were immature at this age.

In Table 3 the entire material has been assembled for each age group. Since large-sized as well as small-sized experiments are entered here, the reproduced figures ought to give a good general idea of the average age for maturity in this form of trout. A comparison of this Table with Table 2 shows likewise that the sex ratio has on the whole been fairly normal, though with a small preponderance of the males.

Growth and length within the different maturity groups

In connection with the different experiments so far only the percentage or the number of mature males and females has been discussed for every age group, independent of the age at which maturity had been reached. In the following we shall discuss the continued growth and size of the different maturity groups. In doing so a comparison with Table 2 ought to be made. We begin with experiment F3C which has yielded the richest material, and has shown the smallest losses.

In Fig. 11 we have reproduced the growth curves for the groups of males that have attained maturity during different years. At the age of 3 years there existed here 16 specimens or 4 % of mature males. These can then be traced, although in decreasing numbers, to the age of 9 years. In the course of the tenth year the losses were so high that the group was no longer followed up. At the beginning the average length was 20.4 cms. against 15.4 cms. of the immature specimens of the same age. During all the subsequent years the average length of these specimens which first had reached maturity was greater than that of the other groups of mature males. At the age of 8 years, when 13 of the original 16 specimens were still in existence, the average length amounted to 41.5 cms., and at the age of 9 years to 42.8 cms.

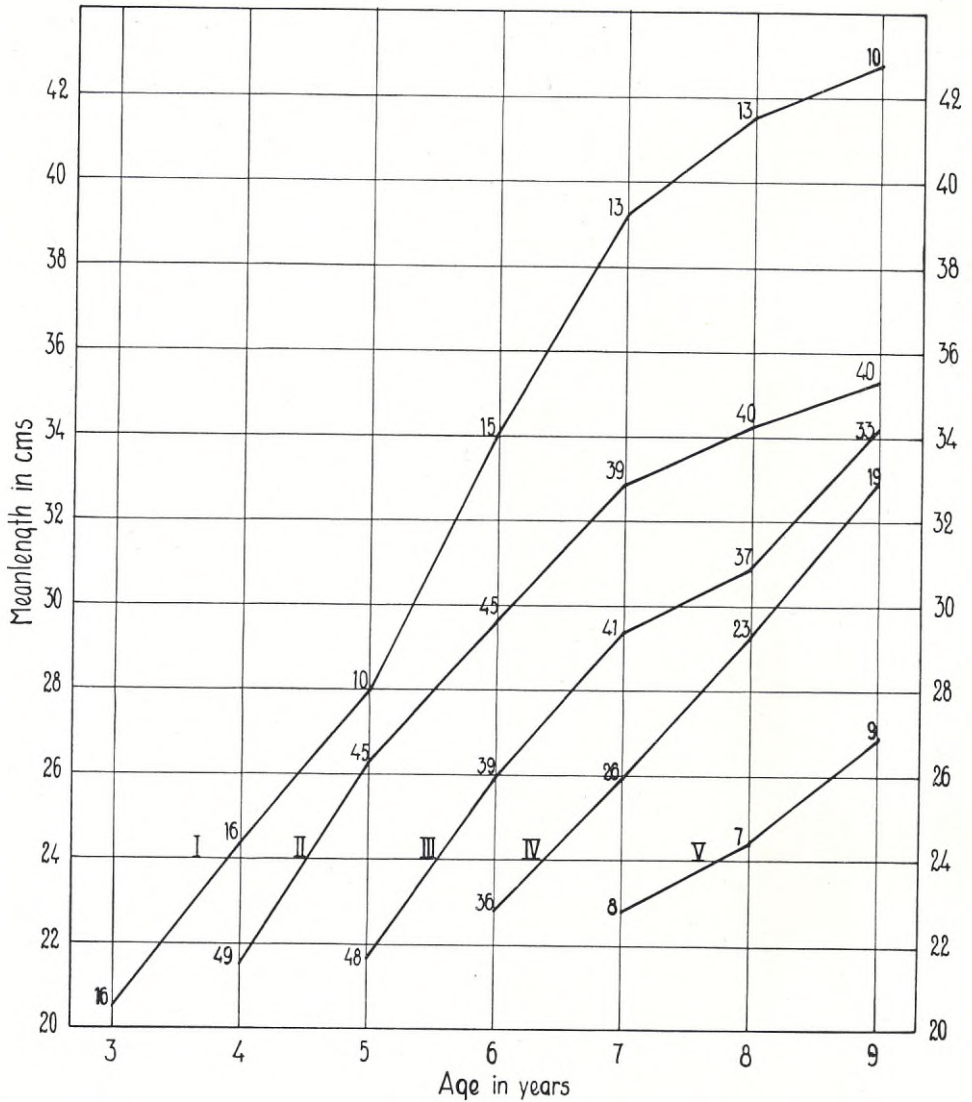


Fig. 11. Small river trout. Relation between age at maturity and growth rate in the males in exp. F3C. The figures at the curves indicate the number of specimens.

From among the just mentioned specimens that were immature at the age of 3 years 49 males reached maturity during the following year, thus at the age of 4 years. Their average length was 21.5 cms. as against 15.6 cms. of the still immature specimens and 24.4 cms. of the males that had been mature already at the age of 3 years. Also in the continuation the average length of the males, mature at 4 years, was constantly greater than that of the specimens that became mature at a greater age. The growth of this

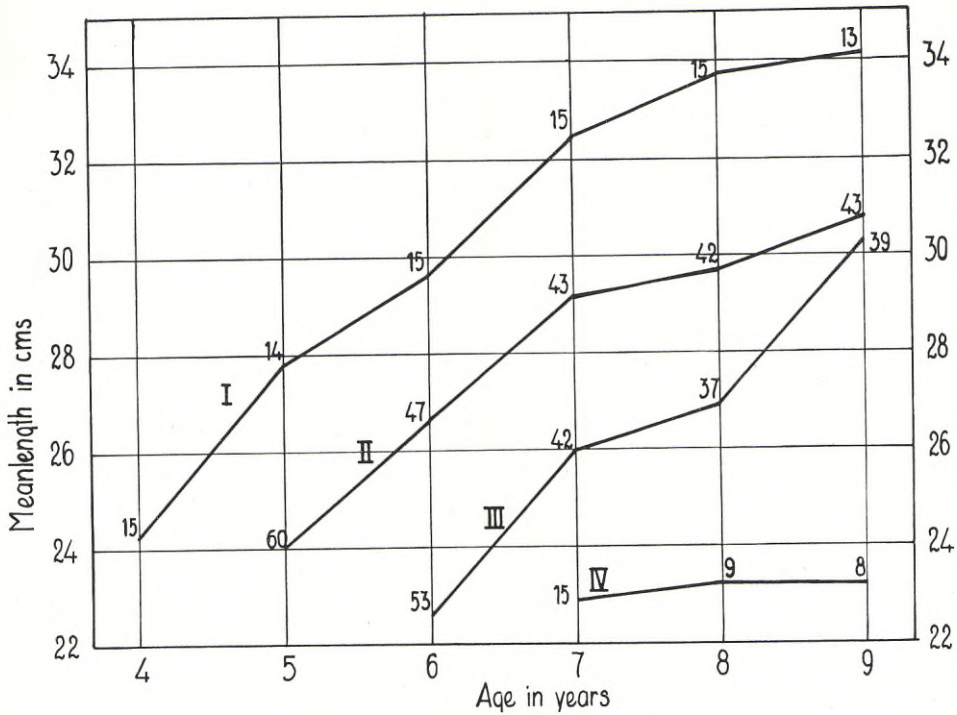


Fig. 12. Small river trout. The same as in Figure 11, but in the females.

group of mature specimens was, however, poorer, their average length at the age of 9 years, when 40 individuals of the original 49 were still in existence, being 35.3 cms. The diagram exhibits the same result also for the 48 specimens that became mature at the age of 5 years, and for the 36 specimens that reached maturity at the age of 6 years. The average length at maturity was slightly greater than what it had been in the preceding year for the specimens that then reached maturity, but remained for each group behind that of the specimens that had earlier become mature, and now were of the same age. At the same time it surpassed that of the still immature specimens. And also in the continuation the remark applies which has been made for the specimens that had become mature at the ages of 3 and 4 years, viz. the average length was all the time smaller than that of the specimens of the same age that had, however, reached maturity earlier. It can be mentioned that this applies also to a smaller number of males (8 specimens) that reached maturity only at the age of 7 years.

Fig. 12 shows the corresponding conditions for the females. Also here the average length of the specimens that had reached maturity with growing age was smaller for every age than that of the specimens of the same age that had reached maturity at an earlier age. The growth was, however, poorer throughout than in the males. The average length of the specimens that

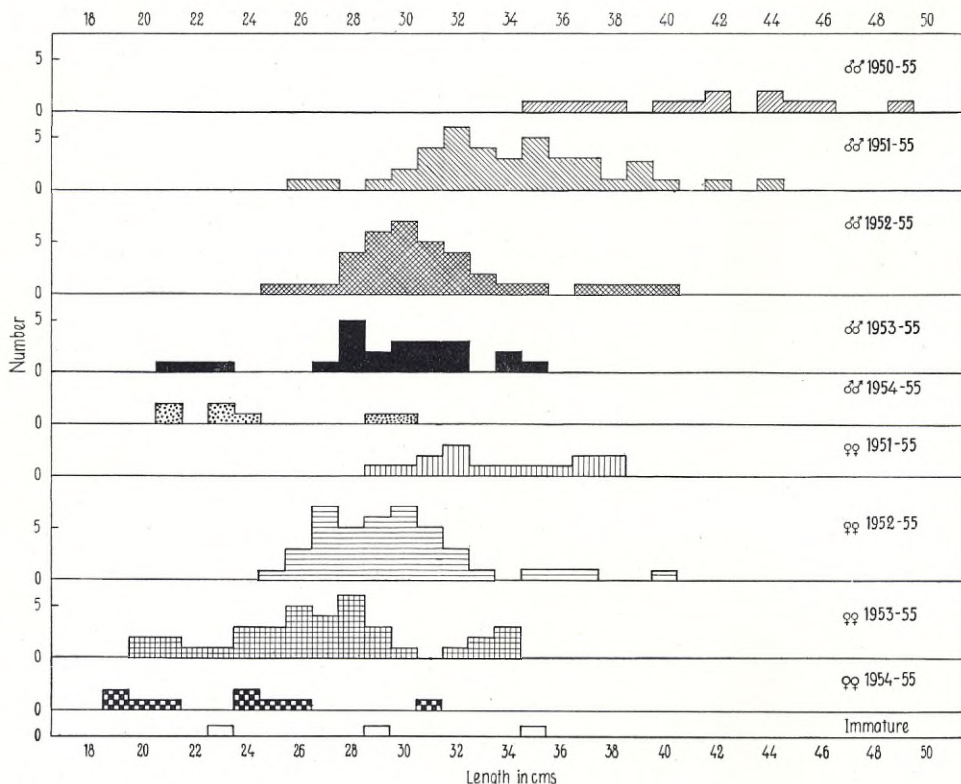


Fig. 13. Small river trout. Number and size distribution of males and females in exp. F3C, matured at different ages, but all of them now 8 years old.

reached maturity in a certain year was furthermore as a rule smaller than what it had been in the previous year in the specimens that then became mature.

Fig. 13 supplements Figs. 11 and 12, and has been included in order to show the size distribution at growing age in the different maturity groups. It illustrates very clearly what has been said about the continued growth in these groups. The specimens that have become mature at the earliest age lead all the time before those that had reached maturity a year later, and these in turn before those that had been another year older, when reaching maturity, etc. The great spreading leads, however, to a partial overlap of the different groups. In the cases, where a certain group comprises a greater number of specimens, the size distribution is, however, expressed by more or less typical binominal curves.

What has been said here shows furthermore that the specimens reaching maturity in a certain year must be found among the larger individuals out of the specimens that were immature a year earlier. Still more important

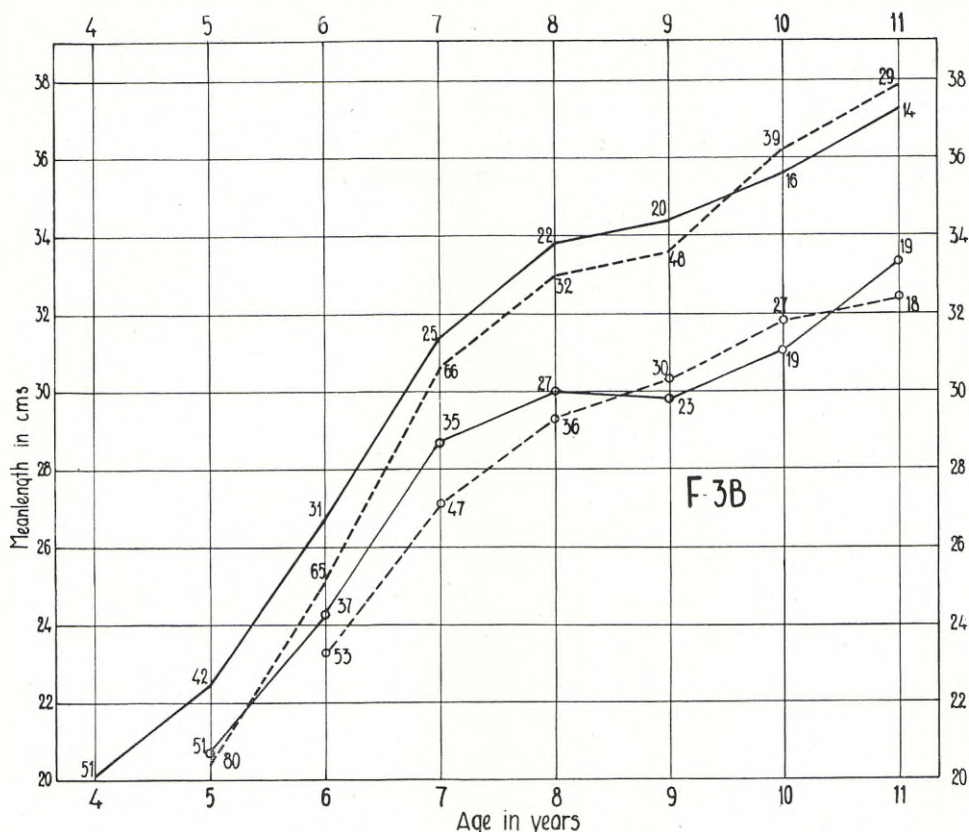


Fig. 14. Small river trout. Relation between age at maturity and growth rate in males and females in exp. F3B. —○— = ♂, ○---○ = ♀.

Table 4. *Small river trout*. Mortality in the more important experiments (Losses in different years as percentage of the number in the previous year).

Age	Experiments							Mean
	F 2 A	F 2 B	F 2 C	F 4	F 3 A	F 3 B	F 3 C	
3	21.3	5.5		20.3	43.1	18.8	13.9	23.5
4	17.9	33.0	5.9	25.1	9.0	2.5	12.5	15.1
5	6.3	27.1	31.5	42.6	20.4	11.0	13.3	21.7
6	—	13.1		27.6	14.6	19.8	11.4	17.3
7	—	—	—	18.4	9.0	3.1	14.6	11.3
8	—	—	—	—	—	23.3	9.1	16.2
9	—	—	—	—	—	11.7	6.6	9.2
10	—	—	—	—	—	18.0	32.2	25.1
11	—	—	—	—	—	17.1	—	17.1
Total	39.6	52.1		79.7	68.0	74.8	71.8	—
Years	3	4		5	5	9	8	—

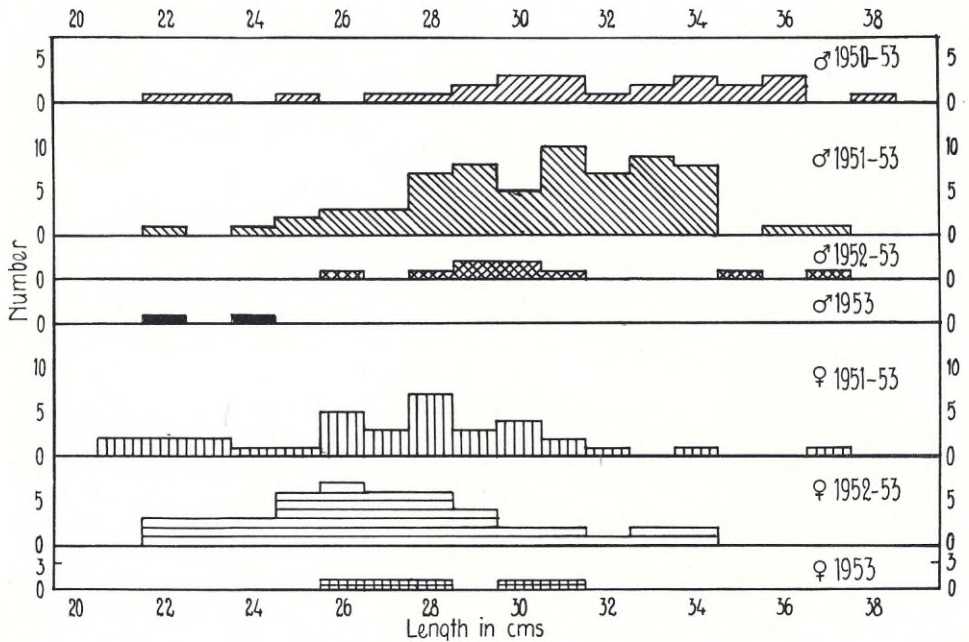


Fig. 15. Small river trout. Number and size distribution of males and females in exp. F3B, matured at different ages, but all of them now 7 years old.

is the fact, which deserves to be specially stressed, that these specimens also in the continuation have throughout exhibited a better growth than the specimens that had become mature later, or that they in any case had retained their lead in size. We shall return to this point after having discussed also the other experiments.

Fig. 14 illustrates the growth of the different maturity groups in experiment F3B. Here only two groups, each of males and females, contained a number of specimens sufficient for inclusion. The tendency was the same as in experiment F3C. Here the differences in size between the different groups were, however, smaller, and with increasing age the growth curves became more irregular, and intersected each other. This is explained by fairly large losses during the later years, when the disappearance of specimens of more extreme size produces a deviation of the average length in one direction or the other. As in previous experiments the growth of the females was poorer than that of the males. Fig. 15 shows the distribution of the different groups over different lengths.

Fig. 16 exhibits the results of experiment F4. Also in this experiment only two groups of either sex contained a larger number of specimens. Here the growth curves for the different maturity groups reminded very much of those in experiment F3C. Year after year they kept at a fairly large distance from each other, indicating a continued lead in growth of the specimens

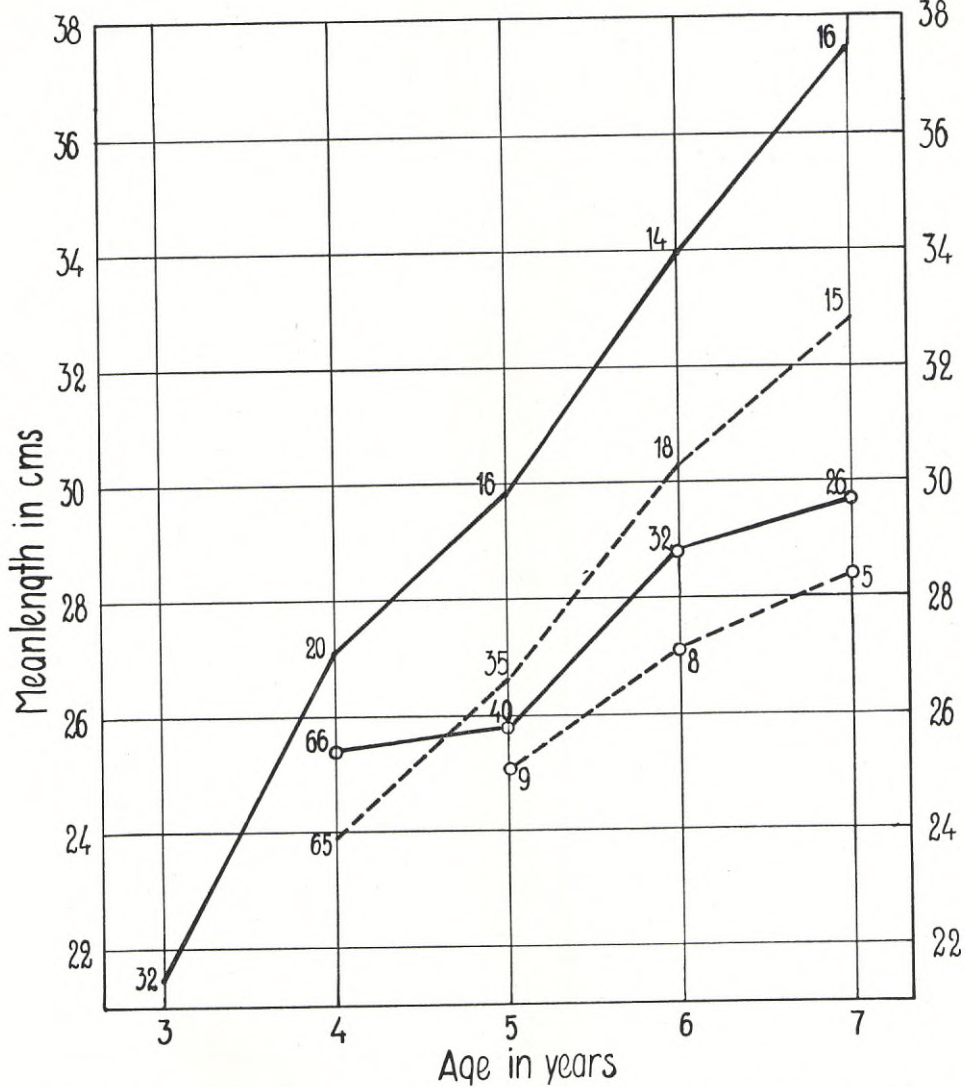


Fig. 16. Small river trout. Relation between age at maturity and growth rate in males and females in exp. F4. — = ♂, ○—○ = ♀.

that had reached maturity earlier. Particularly striking was the very good growth of the males, that had become mature at the lowest age. The diagram shows in addition the poorer growth of the females. The displacement of average length at maturity agreed entirely with that in previous experiments. The size distribution is illustrated in Fig. 17 which also shows the increase in size in these groups from five to six years.

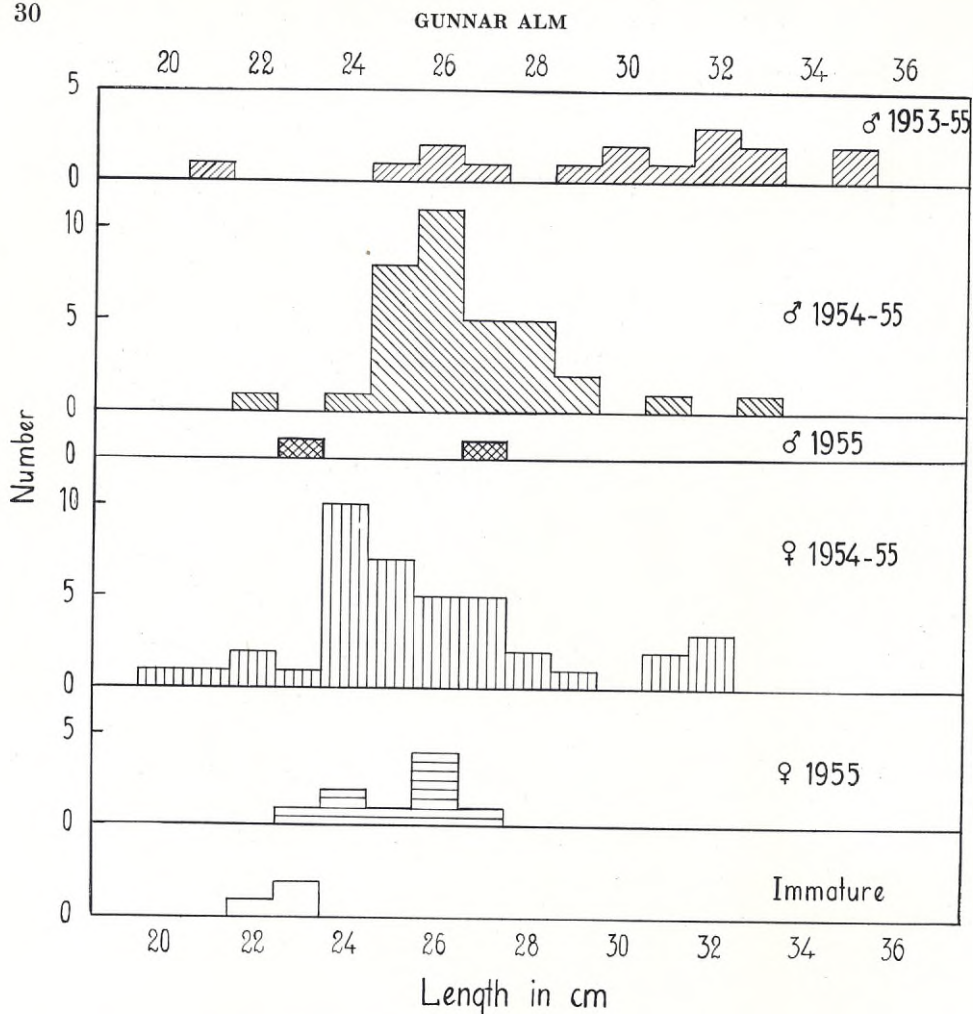


Fig. 17 a.

Fig. 17. Small river trout. Number and size distribution of males and females in exp. F4, matured at different ages, but all of them now a=5, b=6 years old.

Annual or omitted spawning

The yearly examination of all specimens in a certain experiment, which has been very painstaking for this form of trout, has made it possible to establish, whether or not the specimens that had been mature in a certain year were ripe and did spawn every year. This was found to be the case in this form of trout, apart from a few exceptions. Only two males and altogether some ten females in all the experiments were without roe or milt in an succeeding year. As no individual marking had been carried out, it was not possible to establish, whether these isolated specimens were still alive and again ripe in the following year or had died.

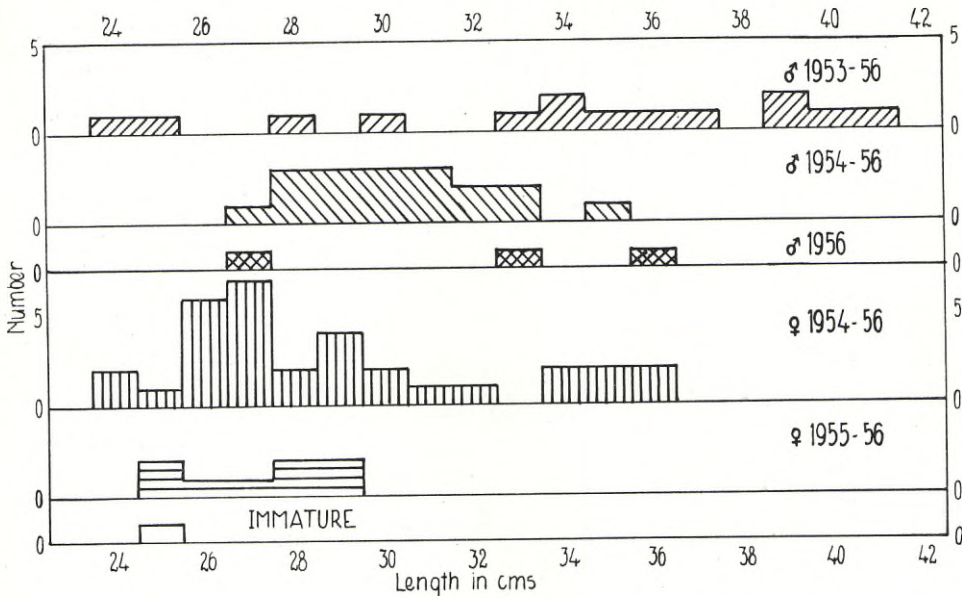


Fig. 17 b.

Mortality

The figures given in Table 2 for the number of specimens entering into every experiment and at every age have been used for the calculation of the percentages of mortality during different years. The obtained figures have been assembled in Table 4. In this Table experiments with better growth are found in the columns of the left side, those with poorer growth on the right.

Table 5. *Small river trout*. Mortality in different maturity groups. (Losses at termination of the experiments in percentage of the number at maturity.)

Experiments	Age at first maturity	Number of				Mortality in %		Number of years between maturity and termination
		♂		♀		♂	♀	
		Maturity	Termination	Maturity	Termination			
F3C	3	16	10	—	—	37.5	—	6
	4	49	40	15	13	18.4	13.3	5
	5	48	33	60	43	31.5	28.4	4
	6	36	19	53	39	47.2	26.4	3
	7	8	8	15	8	—	46.7	2
F3B	4	51	14	—	—	72.6	—	7
	5	80	29	51	19	63.8	62.8	6
	6	—	—	53	18	—	66.0	5
F4	3	32	16	—	—	50.0	—	4
	4	65	15	66	26	76.9	60.6	3
	5	—	—	9	5	—	44.4	2

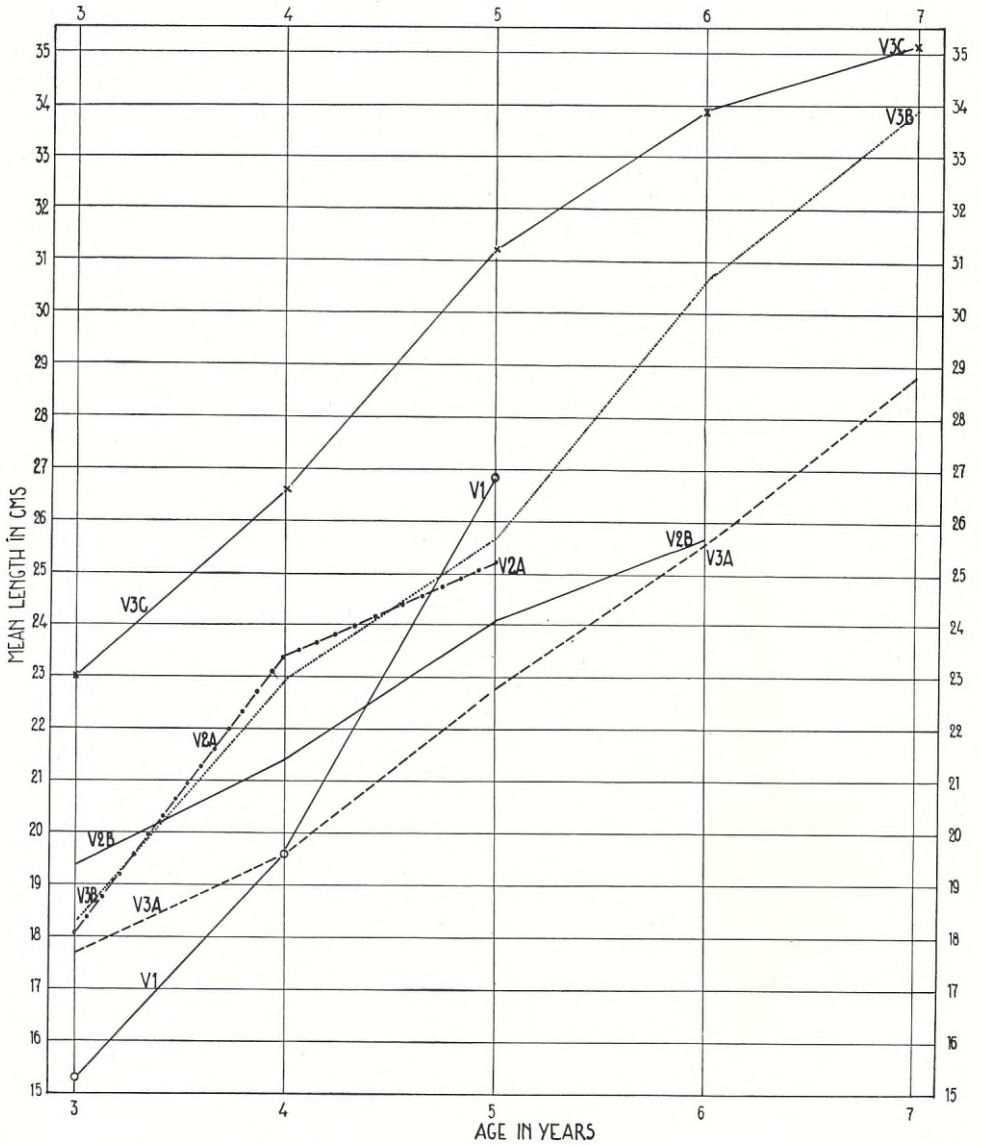


Fig. 18. Big trout from Lake Vättern. Rate of growth in the most important experiments.

The losses have on the whole been rather large, and only experiment F3C shows, with the exception of the last year, a rather low mortality throughout. Otherwise mortality in a certain experiment was sometimes high, sometimes low. In this connection it has to be kept in mind that the experiments have been started in different calendar years, and that thus the age figures do not refer to the same calendar year. The material does not exhibit any obvious

connection of the percentages of losses and better or poorer growth, or lower or higher age.

Of greater interest than these general figures for the losses are those for the losses within the different maturity groups in the experiments, where they have been studied in greater detail. The above discussed Figs. 11, 12, 14, and 16 contain figures for the number of specimens in every group and for every year. On the basis of these figures we have entered into Table 5 figures for the percentages of losses sustained between the maturity of each group and the termination of the experiment. The right-hand column of the Table contains the years to which the numbers of losses refer. If any conclusions can at all be drawn from these figures, they would indicate that the losses from among the specimens that had reached maturity at an early age were at all events not higher than those among the specimens that became mature at a higher age. And since the number of years to which the percentage of losses refers diminishes with increasing maturity age, the figures are rather suggestive of greater losses among the later maturity groups. With regard to the sexual difference the percentage figures might possibly suggest a somewhat greater mortality in the males. Tables 2 and 3 show, however, that at a higher age, i.e. when at all events all males and the majority of the females have reached maturity, the number of males amounts to about 50 % and sometimes more of all specimens. This does thus not favour the idea of any difference between the sexes with regard to mortality.

2. Big brown trout from Lake Vättern

Table 6 contains a compilation of the results of the experiments with big brown trout from Lake Vättern. The material was not as abundant as in the case of the small river trout. It has nevertheless been possible also here to influence growth by a different intensity in the stocking of the ponds or by the use of ponds of different sizes, and thus to obtain experiments which during a sequence of years exhibited throughout better (V3B, V3C) or poorer (V2B, V3A) growth (Fig. 18). Attention has to be paid to the fact that during the first two years experiments V3B and V3C had together formed experiment V3BC. First at the age of 2 years the latter was split with different population densities in different ponds leading to differences in growth rate. Also experiment V3A was split into two experiments during the 7th year, viz. V3Aa containing 150 specimens of 17—20 cms. and V3Ab with 260 specimens of 21—44 cms. These groups were then kept in different ponds.

The length of mature and immature specimens of the same age within a certain experiment

Into Fig. 19 have been entered figures for the average length of mature males and females, and of immature specimens in the different experiments,

Table 6. *Big trout from Lake Vättern. Length and maturity at different ages.*

Exp.	Age	Total numb.	Percentage of number			Mean length in cms.				Year of exa- min.
			Mature		Im- mat.	Total	Mature		Im- mat.	
			♂	♀			♂	♀		
V1	2	262	—	—	100	Ab. 12.0	—	—	Ab. 12.0	1935
V4A	2	182	—	—	100	12.0	—	—	12.0	1958
V3A	2	631	—	—	100	12.3	—	—	12.3	1949
V2A	2	148	—	—	100	13.4	—	—	13.4	1940
V4B	2	110	5	—	97	14.0	15.5	—	13.7	1958
V2B	2	211	—	—	100	14.4	—	—	14.4	1941
V3BC	2	408	6	—	94	14.6	15.7	—	14.5	1952
V4C	2	88	12	—	88	16.4	17.0	—	16.3	1958
V1	3	139	—	—	100	15.3	—	—	15.3	1936
V3A	3	575	3	—	97	17.7	21.9	—	17.5	1950
V2A	3	103	7	—	93	18.1	23.1	—	17.7	1941
V3B	3	191	16	—	84	18.3	18.2	—	18.3	1953
V2B	3	207	10	0.5	89	19.4	21.6	23.0	19.2	1942
V3C	3	105	11	—	89	23.0	22.8	—	23.1	1953
V3A	4	480	13	—	87	19.6	24.3	—	18.9	1951
V1	4	77	16	3	81	19.6	?	?	?	1937
V2B	4	178	14	2	84	21.4	23.2	27.4	21.0	1943
V3B	4	134	40	—	60	22.9	23.0	—	22.9	1954
V2A	4	110	37	3	60	23.4	25.7	28.8	21.9	1942
V3C	4	100	33	9	58	26.6	27.0	28.0	26.2	1954
V3A	5	422	28	1	71	22.8	26.5	—	21.3	1952
V2B	5	139	23	8	69	24.1	23.6	26.6	23.9	1944
V2A	5	84	50	21	29	25.2	25.6	28.6	21.4	1943
V3B	5	125	50	3	47	25.7	25.4	28.0	26.2	1955
V1	5	67	46	6	48	26.9	27.2	29.8	25.1	1938
V3C	5	84	34	20	46	31.2	31.0	31.2	31.3	1955
V3A	6	410	39	7	54	25.6	28.5	33.5	22.6	1953
V2B	6	131	29	8	63	25.7	25.0	31.5	25.3	1945
V3B	6	97	50	19	31	30.6	30.3	31.3	30.6	1956
V3C	6	83	34	38	28	33.9	33.7	34.2	33.7	1956
V3Aa	7	119	33	1	66	22.6	22.7	25.0	22.0	1954
V3Ab	7	245	59	21	20	31.9	32.3	33.1	29.7	1954
V3B	7	92	55	27	18	33.8	33.7	33.6	34.4	1957
V3C	7	76	36	50	14	35.1	34.4	35.5	35.1	1957
V3Aa	8	94	43	12	45	26.5	27.5	26.0	26.8	1955
V3Ab	8	218	62	17	21	33.0	34.8	35.4	31.1	1955
V3C	8	75	32	57	11	35.7	34.3	36.3	36.6	1958
V3Aa	9	77	51	21	28	31.2	30.7	30.7	32.5	1956
V3Ab	9	206	63	21	16	34.7	35.1	36.1	32.1	1956
V3Aa	10	67	63	31	6	32.8	32.2	34.1	34.8	1957
V3Ab	10	168	66	26	8	37.0	36.8	37.7	37.2	1957

all with increasing age. Contrary to what is the case in the small river trout the growth of the males in this form of trout was not better than that of the females. In several experiments the average length of the latter was greater than that of the males of the same age. In other cases growth was rather much the same in either sex. The latter applies especially to the experiments V3B and V3C with good and very good growth, respectively. Here the average

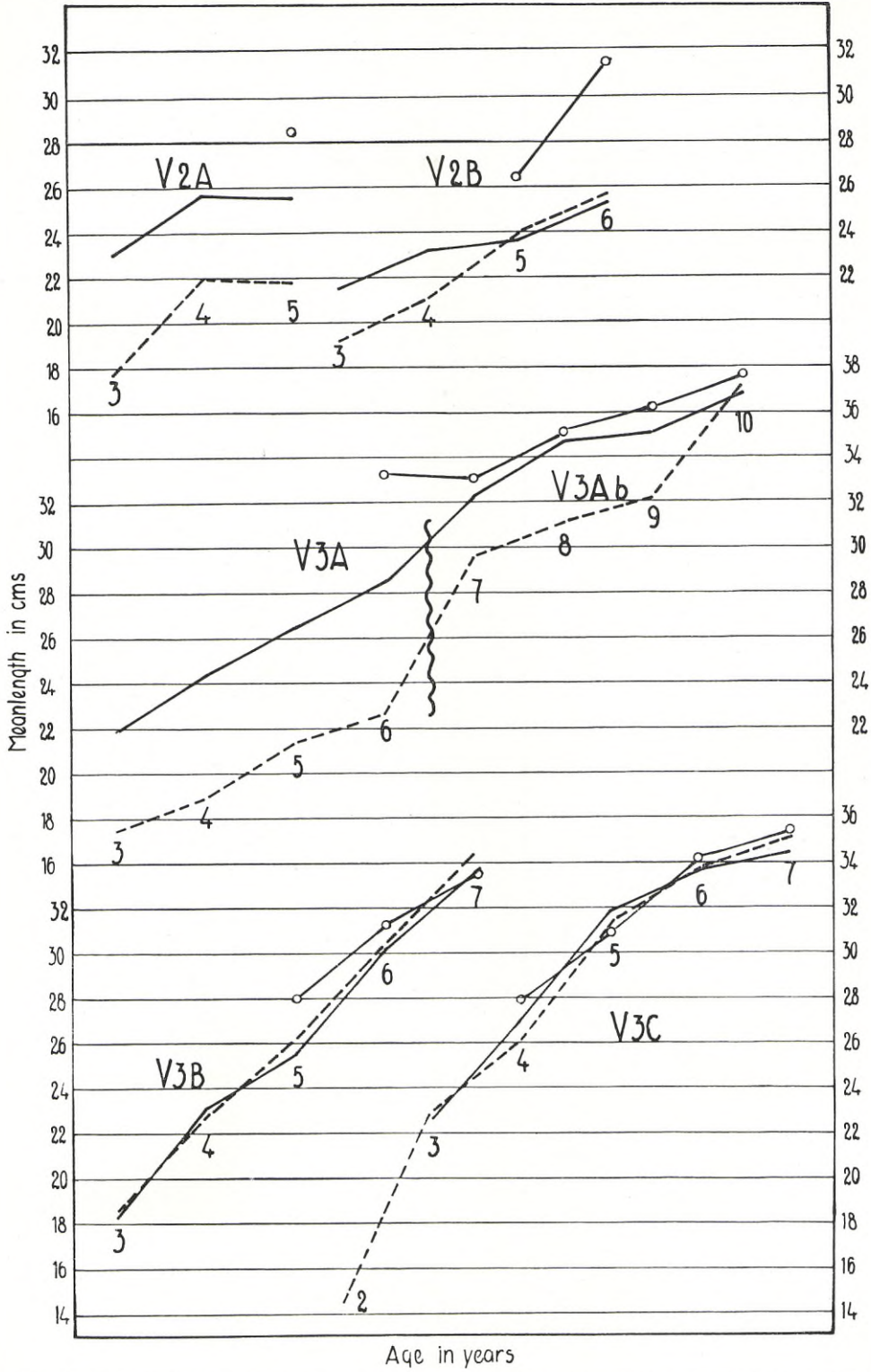


Fig. 19. Big trout from Lake Vättern. Mean length of mature males and females and of immature specimens. — = mature ♂, ○—○ = mature ♀, - - - - = immature specimens. The figures at the growth curves indicate the age.

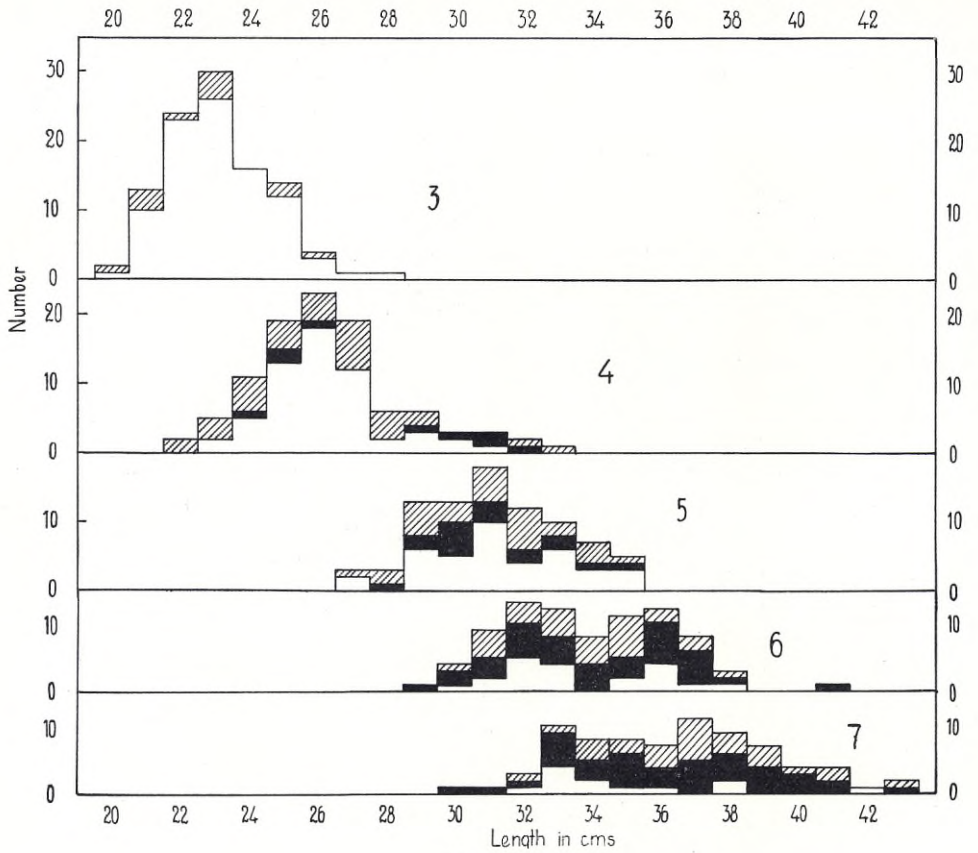


Fig. 20.

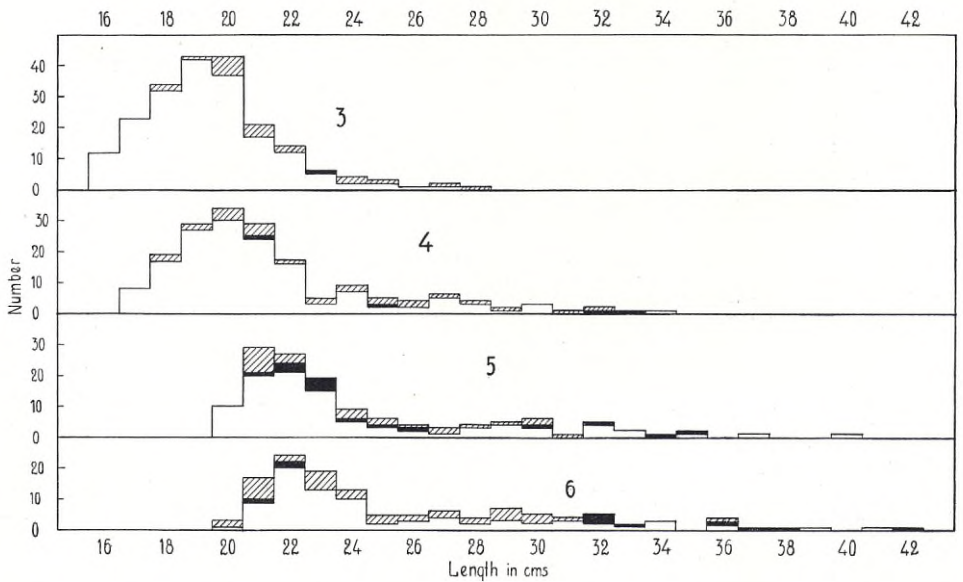


Fig. 21.

Figs. 20—22. Big trout from Lake Vättern. Number of mature males and females and of immature specimens in different size groups at different ages in a fast-, a medium-, and a slow-growing experiment. Fig. 20 — exp. V3C, Fig. 21 — exp. V2B, Fig. 22 — exp. V3A.

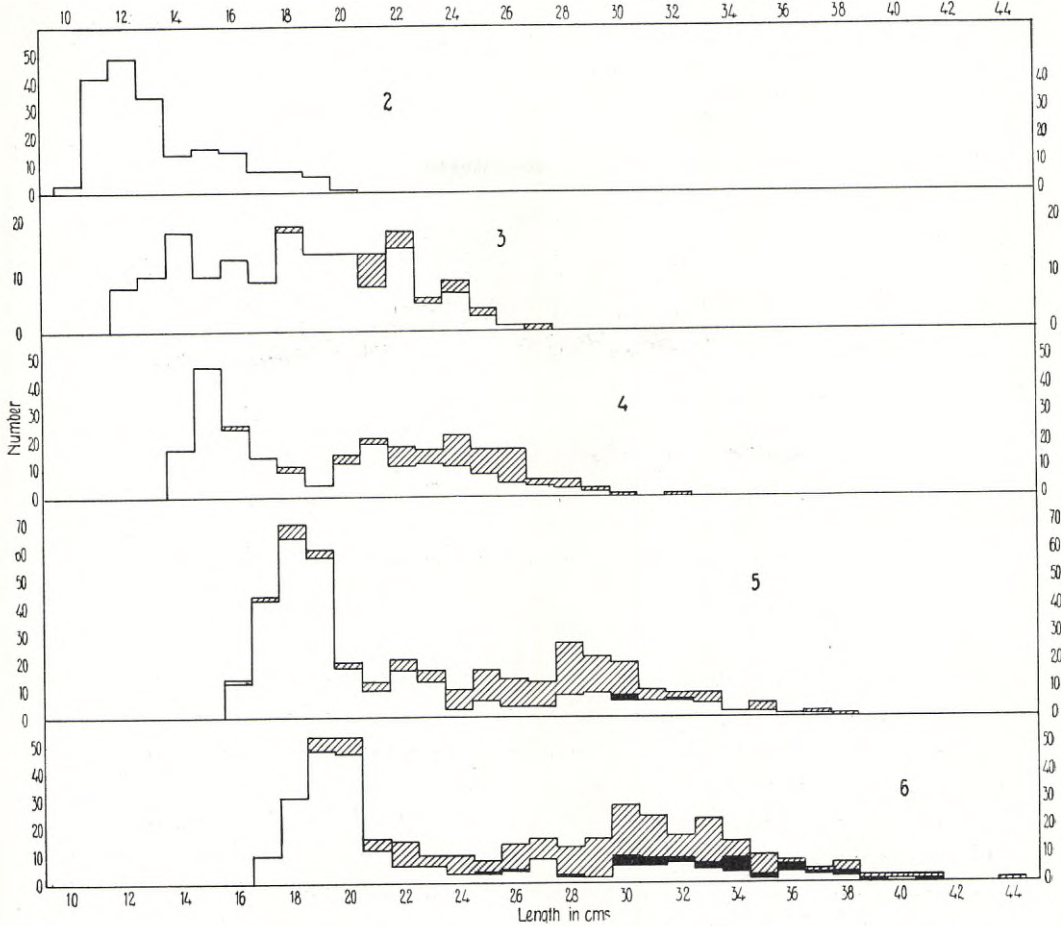


Fig. 22.

length of the immature specimens was at the same time only inconsiderably smaller than that of the mature females while in the other experiments it remained on the contrary much below the later value. This means that in these latter experiments maturity occurred mainly among the bigger specimens, whereas in the former cases its distribution over the different sizes was more uniform. This can possibly have its reason in the fact that in these experiments, where the growth — especially in experiment V3C — was very good, the size also within the smaller length groups was sufficient for the reaching of maturity at the age in question.

In Figs. 20—22 the above-mentioned differences in growth and size of the two sexes become still more evident. In experiment V3C (Fig. 20) with the best growth mature males and females were fairly equally distributed over

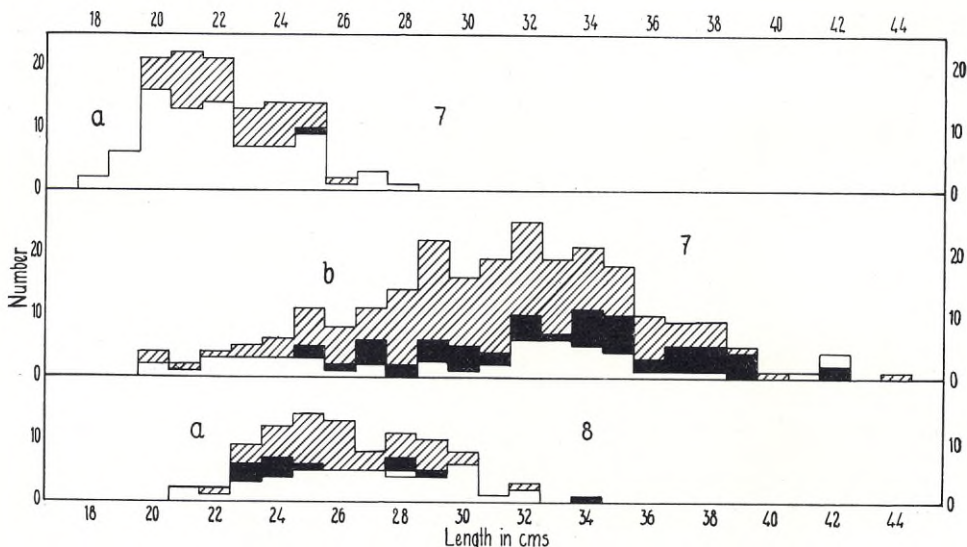


Fig. 23. Big trout from Lake Vättern. Splitting into two length groups.

the different length groups, both at lower and higher age. Experiment V2B (Fig. 21) with medium or, perhaps more correctly, slightly poorer growth exhibits a tendency towards higher maturity among the specimens with better growth rate. At the same time mature females were commoner there. In experiment V3A (Fig. 22) at last with rather poor growth maturity was evidently tied up with the groups of greater length in spite of the fact that numerous immature specimens occurred also among them. The connection between size and maturity is here in complete agreement with the conditions in the small river trout, apart from the fact that the mature females are found mainly among the bigger specimens. It must also be pointed out that in this experiment the size curve exhibited a very wide amplitude of variation, especially towards the groups with greater length, which for the rest was characteristic also for experiment V2B. Yet in experiment V3A the size curve became in addition increasingly double-pointed. As already mentioned above the experiment was split during the 7th year according to the same principles as the already mentioned experiment with small river trout (Fig. 8). The size limit lay between 20 and 21 cms. Fig. 22 shows group a) to have contained only isolated mature males, while in group b) many of them (36 %) and also some mature females (7 %) were found. A year later the size curves coincided in part, but both average length (Fig. 23) and maturity exhibited great differences. Within group a) only 33 % of mature males (average length 22.7 cms.) and one mature female were found. Group b) on the other hand now contained 59 % of mature males (average length

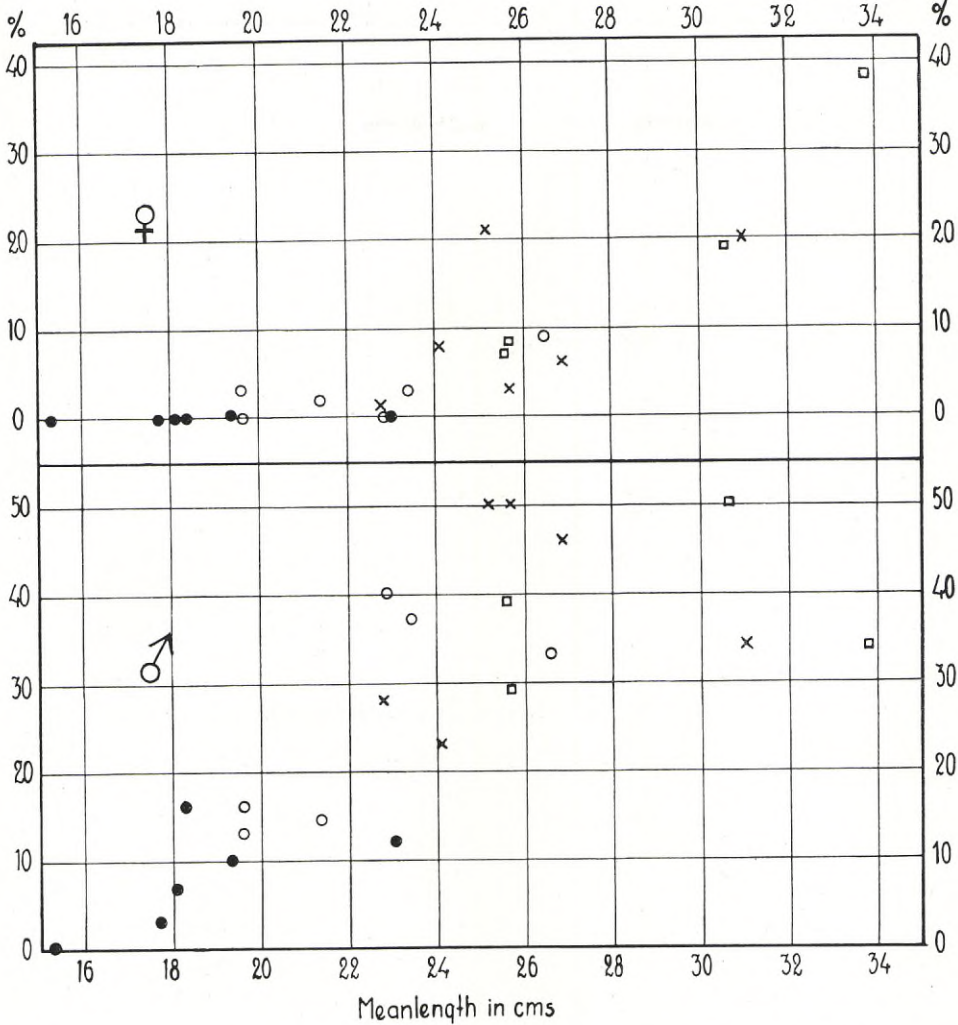


Fig. 24. Big trout from Lake Vättern. Relation between mean length, age, and maturity, ●=3, ○=4, ×=5, □=6 years (summers) old.

32.3 cms.) and 21 % of mature females (average length 33.1 cms.). For the sake of comparison also the size distribution in group V3Aa at the age of 8 years has been included in this diagram. Even then this group had not yet reached the average size shown by group V3Ab at the age of 7 years. It is evidently due to this poorer growth that in spite of the age not more than 43 % were mature males and 12 % mature females. The maturity was thus considerably lower than in group b), when it was one year younger.

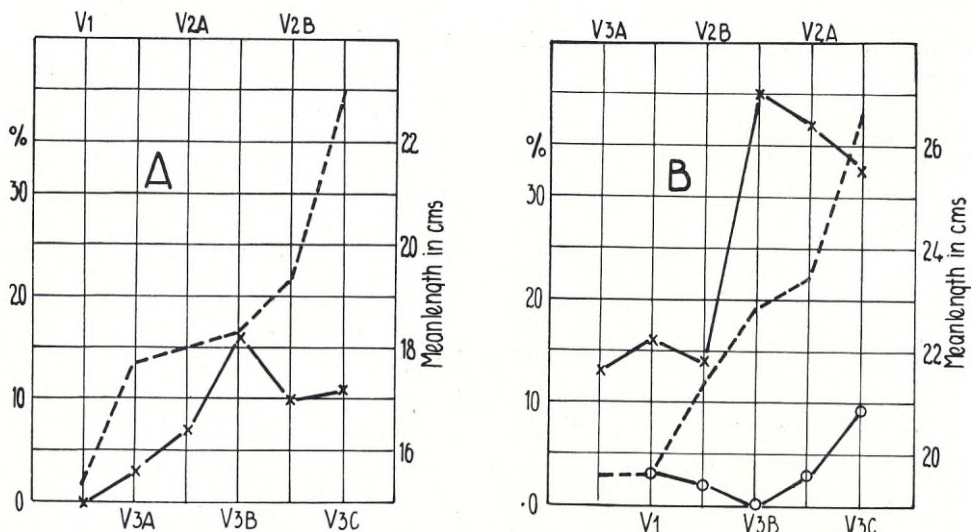


Fig. 25. Big trout from Lake Vättern. Percentage of mature males and females in experiments with A) 3- and B) 4-years old specimens. $\times-\times-\times = \text{♂}$, $o-o-o = \text{♀}$, ----- = mean length in the experiments.

The number of mature specimens of the same age in experiments with better and poorer growth (=year classes with different growth)

Also in this form of trout the results exhibit a distinct connection between the number of mature specimens and the age and average size at a certain age. As can be seen from Fig. 24 the percentage of mature specimens was as a rule greater in experiments with better growth than in others with poorer growth, but of the same age. In this form of trout, however, sexual maturity is reached at a higher age than in the small river trout. This is evident from Fig. 24, but still more from Fig. 25. In certain experiments a rather great number of males was still immature at the age of 5 and even of 6 years.

Table 7. *Big trout from Lake Vättern*. Number of mature males and females at different ages.

Age	Mature				Immature	
	♂		♀		Number	%
	Number	%	Number	%		
3	85	6.4	—	—	1.235	93.6
4	225	20.9	18	1.7	836	77.4
5	312	33.8	56	6.1	553	60.1
6	273	37.8	93	12.9	355	49.3
7	262	49.3	115	21.5	156	29.2
8	192	49.6	97	24.8	98	25.6
9	168	59.4	60	21.2	55	19.4
10	152	64.7	66	28.1	17	7.2

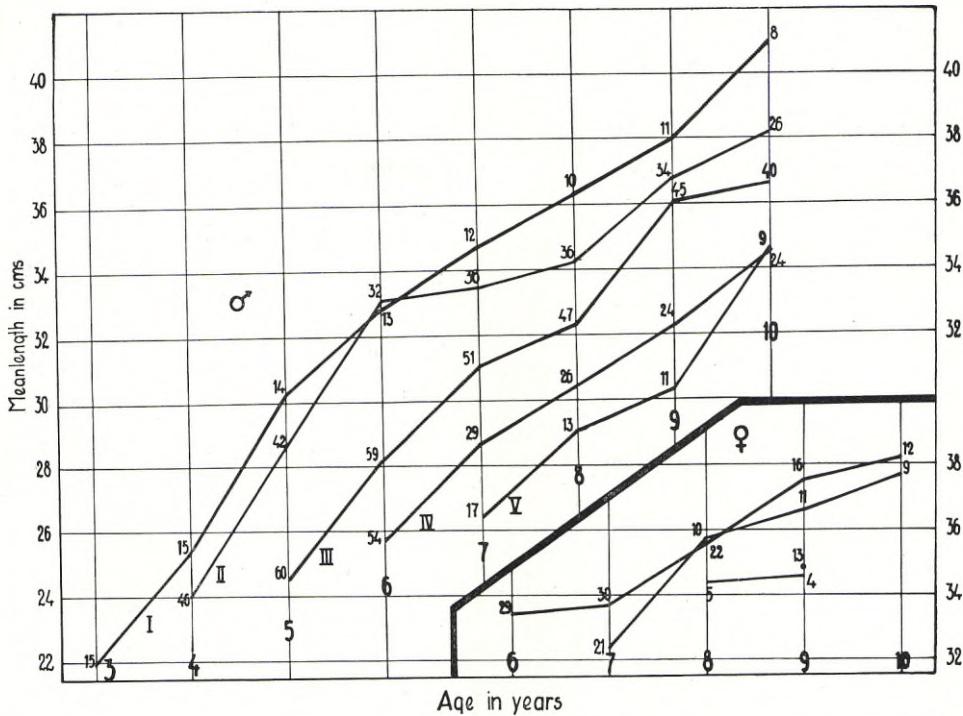


Fig. 26. Big trout from Lake Vättern. Relation between age at maturity and growth rate in males and females in exp. V3A.

It must, however, be pointed out that in some experiments with particularly good growth a number of mature males were found already at the age of 2 years. Among 3-years-old females only one specimen was mature in one experiment. Also at the age of 4 and 5 years mature females were scarce or altogether missing. Even at the age of 6 and 7 years a great number of the females was still immature. The higher percentage of mature females is in obvious connection with the average size of all specimens in the experiment. Yet, certain exceptions from this connection do occur. Thus experiment V3C exhibited, in spite of very good growth, a low percentage of mature males. This probably derives from the fact that here the females formed a majority, at the ages of 7 and 8 years the mature females amounting to 50 and 57 %, respectively. Experiment V3B exhibited on the contrary a high percentage of males and a correspondingly low percentage of mature females at the age of 4 and 5 years. In experiment V2A the percentage of mature males and still more so that of mature females was unusually high, and this in spite of the fact that the growth was only of medium rate.

As for the small river trout we have assembled the figures for maturity at

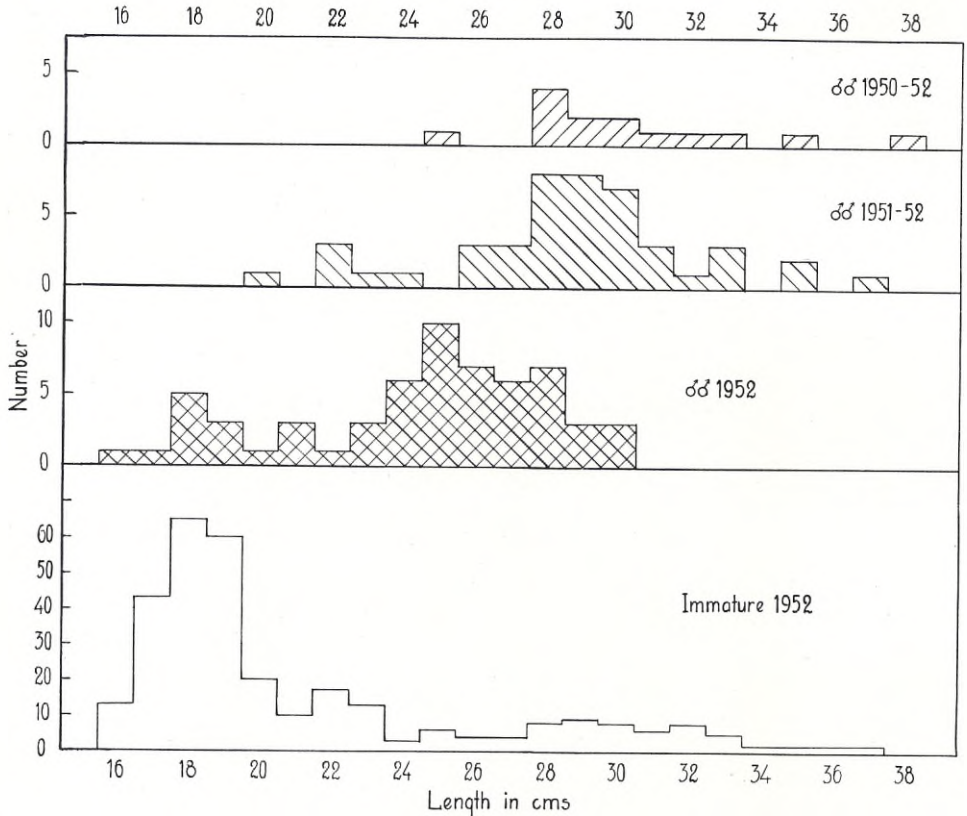


Fig. 27. Big trout from Lake Vättern. Number and size distribution in exp. V3A of males and females, matured at different ages, but all of them now 5 years old.

different ages from all experiments also for the big trout. Thus Table 7 shows still more clearly the difference in the age for maturity in these two forms of trout.

Growth and length within the different maturity groups

In earlier experiments with this form of trout (V1, V2A, and V2B) the different maturity groups have not been kept apart. This has, however, been done to a large extent in some later experiments. Fig. 26 thus shows that the gradually and with increasing age mature males in experiment V3A and later V3Ab in the continuation have exhibited a growth which entirely agrees with that of the small river trout. Thus the average length of the males that had become mature at an earlier age lay in the continuation all the time above that of the males that had reached maturity a year later. This applies, though less clearly, also to the females. The average length of the males that had become mature at a higher age was furthermore greater than the

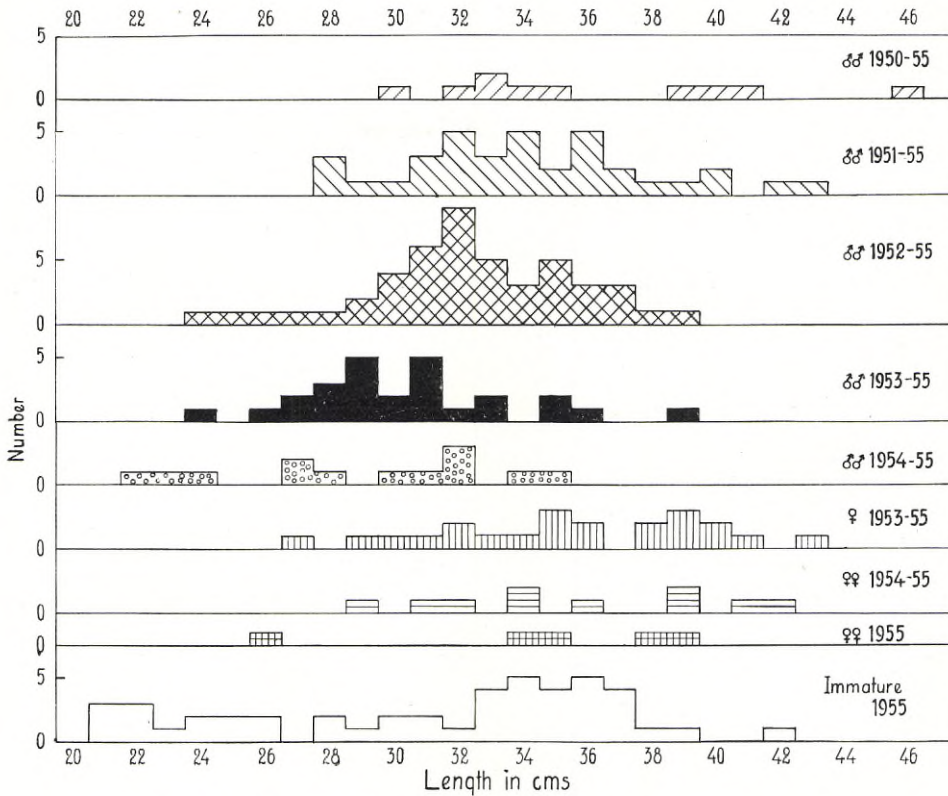


Fig. 28. The same as in Fig. 27, but all of them now 8 years old.

average length of the males when they were mature a year earlier. This agrees also entirely with the conditions in the small river trout. Figs. 27 and 28 give further information about size and distribution within the different maturity groups at the ages of 5 and 8 years.

In Fig. 29 for experiment V3B the difference in size between the three male maturity groups is less evident than in experiment V3A, but the tendency is the same. Thus in either experiment the larger males in each age group were the first to reach maturity. In experiment V3A this applied also to the females. In experiment V3B, however, the females exhibited a different behaviour, their growth being poorer in the continuation, provided that the scanty material permits the drawing of any conclusions. This circumstance had the result that the females that were mature at a certain age were smaller after the lapse of one year than the females that then reached maturity. The growth curves for the females that had become mature at a greater age lay therefore above those of the females that had reached maturity at an earlier age. The same conditions existed in the other experiment with good growth, V3C, see Fig. 30. Unfortunately the maturity groups of the

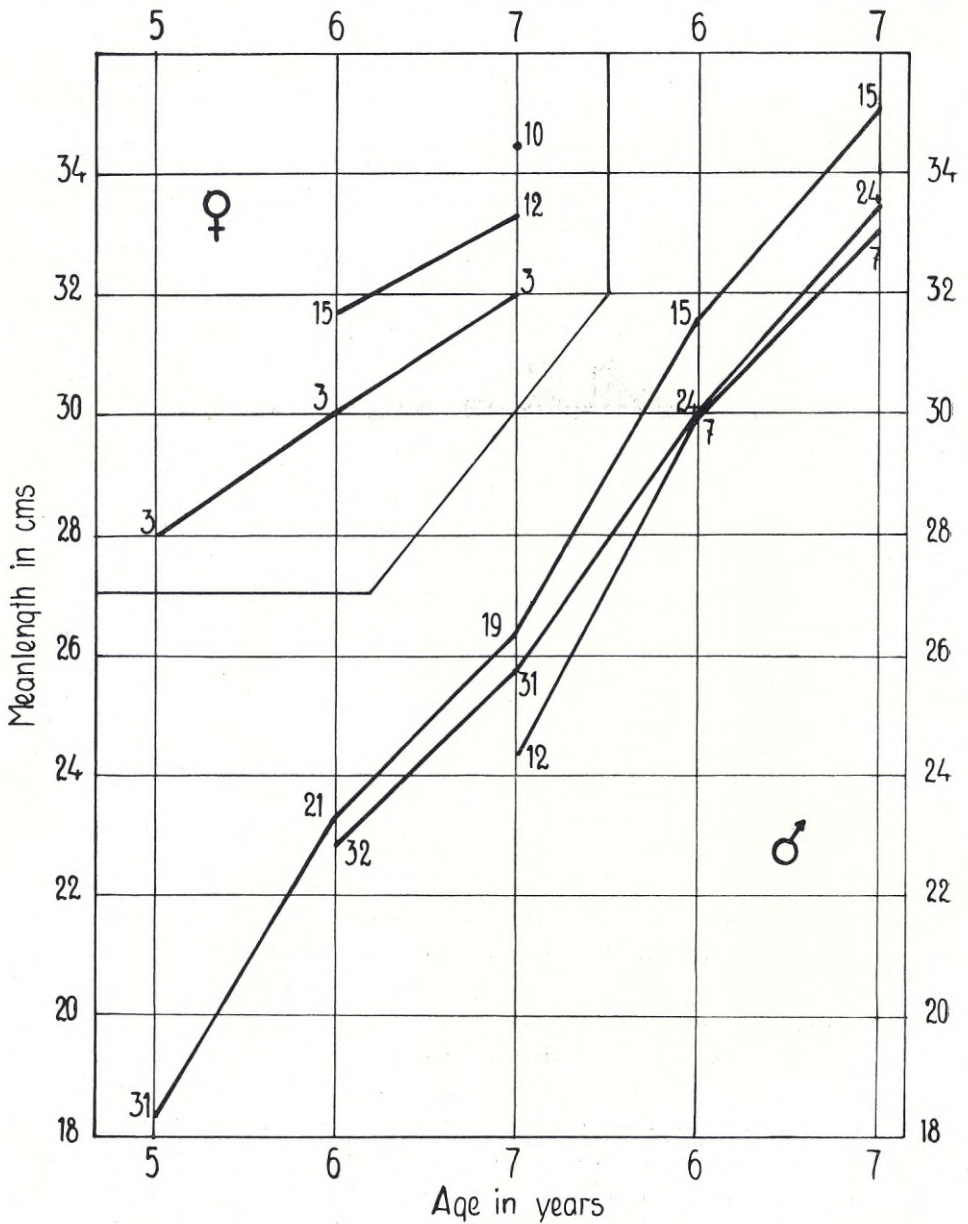


Fig. 29. Big trout from Lake Vättern. Relation between age at maturity and growth rate in males and females in exp. V3B.

males were not kept apart here. These differences in size of the female maturity groups in experiment V3A on the one and in experiments V3B and V3C on the other hand explain the differences in average length of mature and immature specimens in the different experiments.

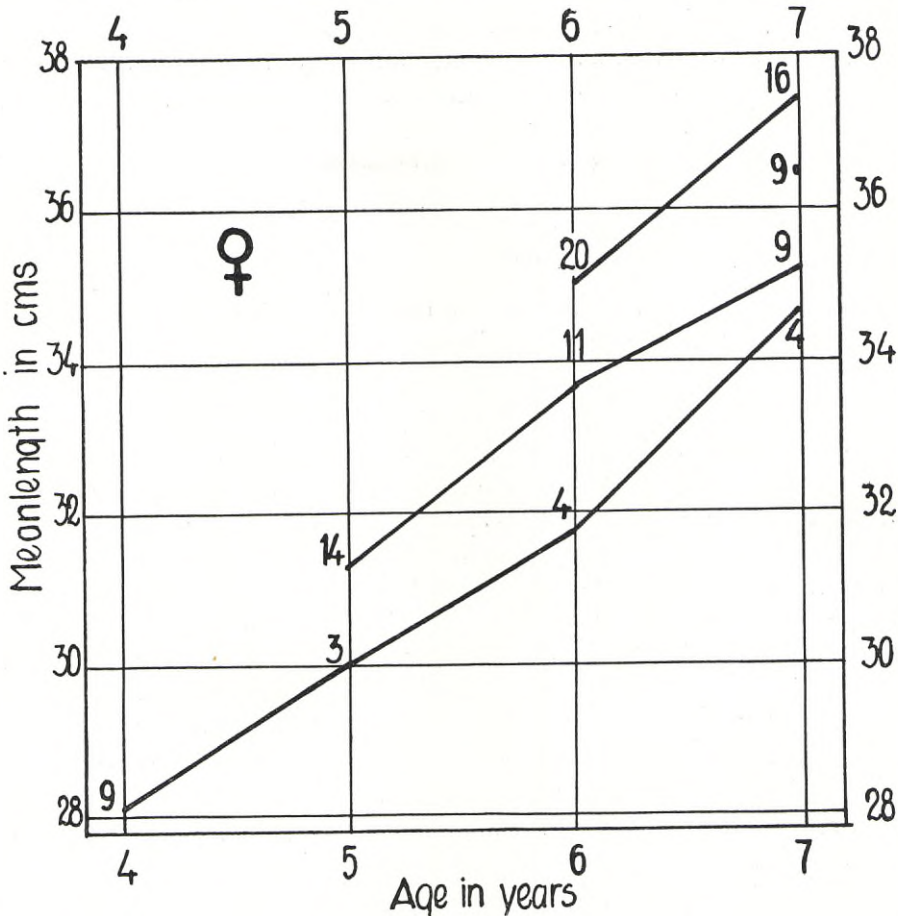


Fig. 30. Big trout from Lake Vättern. Relation between age at maturity and growth rate in females in exp. V3C.

Annual or omitted spawning

Earlier experiences from investigations in the field and from the rearing of different forms of trout have shown that the large forms do not spawn every year, but often omit a year (ARVIDSSON 1935, ALM 1950, RUNNSTRÖM 1952). On account of the required speed not all experiments with the form of trout now in question have always been examined with regard to renewed spawning, but have only been checked with regard to the different maturity groups. Only the experiments V3Aa and V3Ab have been carefully controlled in this respect. Table 8 shows the results. Especially among the females the spawning has been omitted much more frequently than has been the case with the small river trout. In these experiments altogether about 17 % of the earlier mature females have not spawned during a subsequent year.

Table 8. *Big trout from Lake Vättern*. Number of earlier mature specimens not spawning in a following year. Number of last year mature specimens in brackets.

Age in years	V 3 A a		V 3 A b	
	♂	♀	♂	♀
7	0 (16)	—	1 (128)	4 (30)
8	8 (32)	—	1 (132)	3 (32)
9	1 (33)	1 (14)	0 (127)	5 (31)
10	8 (39)	6 (15)	0 (110)	5 (22)

Mortality

Table 9 shows the percentage of losses for all experiments with this form of trout at different ages. No regularity can be traced in the figures for the losses. The mortality might, however, have been fairly low in experiment V3C with the best growth, but also experiment V3A with poor growth exhibited in certain years a rather low mortality. After the splitting-up of this experiment in the course of the 7th year the mortality was higher in experiment a, where the size was smaller than in experiment b. On lumping the entire material together the mortality of this form of trout is found to have been somewhat lower throughout than in the small river trout.

Into Table 10 the figures for the losses of the different maturity groups in the experiments V3A and V3B have been entered. These figures are as irregular as for the small river trout. Thus the values are on the whole as high for the older as for the younger maturity groups. As, however, the number of years to which the values for the losses refer has been greater in the later case, the possibility exists that the mortality has been greater among

Table 9. *Big trout from Lake Vättern*. Mortality in the more important experiments. (Losses in different years in per cent of the number in the previous year.)

Age	Experiments								Mean
	V3C	V3B	V1	V2a	V2b	V3A	V3Aa	V3Ab	
3	—	—	46.5	30.4	1.9	8.9	—	—	19.1
4	4.8	13.4	44.6	25.7	14.0	16.5	—	—	18.8
5	16.0	6.7	13.0	23.6	21.9	12.7	—	—	15.7
6	1.2	22.4	—	—	5.7	2.8	—	—	8.0
7	8.4	5.2	—	—	—	—	20.7	6.1	10.1
8	1.3	—	—	—	—	—	21.0	11.0	11.1
9	—	—	—	—	—	—	18.5	5.5	12.0
10	—	—	—	—	—	—	13.0	18.4	15.7
Total	28.5	51.8	74.4	43.5	37.9	35.0	55.3	35.4	
Years	5	4	3	3	4	4	4	4	

Table 10. *Big trout from Lake Vättern*. Mortality in different maturity-groups. (Losses at the termination of the experiment in per cent of the number at maturity.)

Experiments	Age at first maturity	Number of				Mortality in %		Number of years between maturity and termination
		♂		♀		♂	♀	
		Maturity	Termination	Maturity	Termination			
V3A— V3A a+b	3	15	8	—	—	46.7	—	7
	4	46	28	—	—	39.1	—	6
	5	60	40	—	—	33.3	—	5
	6	54	24	30	12	55.6	60.0	4
	7	17	9	21	9	47.1	57.1	3
V3B	2—3	31	15	—	—	51.6	—	4
	4	32	24	—	—	25.0	—	3
	5	12	7	3	3	41.7	0	2
	6	6	2	15	12	66.7	25.0	1

the specimens that had reached maturity at higher age. This agrees with what has been mentioned above about the small river trout. As in the latter form no obvious difference between the mortality of the two sexes is noticed in the big trout. The figures in Table 6 also show the number of males at higher age to amount to at least 50 % in several experiments.

3. Big brown trout from Switzerland and hybrids between different forms of trout and between trout and salmon

Table 11 contains the results of experiments in part with big trout from Switzerland, reared at Kälärne (roe imported from Denmark), in part with hybrids between small river trout and big trout from lakes, and between salmon and sea trout. For the forms of trout and the hybrids the table shows some isolated males to have reached maturity at the age of 2 years in the experiments A and D which also showed the best growth. At the age of 3 years the number of mature males varied between 3—4 and 11 %, the latter figure referring to experiment Cb. At the age of 2 years the experiment C had been split into two experiments, viz. Ca with 150 specimens in two small ponds and Cb with 435 specimens in 2 large and deep ponds. As the result of the greater space per fish the growth became more vigorous in experiment Cb than in Ca. Also the percentage of mature males was higher in Cb. Of the females some 4-year-old specimens were mature in experiment A, and at the age of 5 years most of the females were mature in the experiments A and B, only about 25 % of all specimens remaining immature. The Table shows the sex ratio to have been different in these experiments so that in experiment A the females dominated among the mature specimens, while they were outnumbered by the males in experiment B.

Table 11. *Different forms of trout and hybrids. Length and maturity at different ages.*

Exp.	Age	Number	Percentage of number			Mean length in cm				Year of exam.
			Mature		Im-mat.	Total	Mature		Im-mat.	
			♂	♀			♂	♀		
Big trout from Switzerland A	2	251	1	—	99	15.3	18.5	—	15.3	1946
	3	234	3	—	97	19.6	22.1	—	19.5	1947
	4	143	13	4	83	25.6	27.4	30.2	25.1	1948
	5	131	33	42	25	31.2	31.5	32.1	29.1	1949
Small river trout ♀ × big trout ♂, B Lake Vättern	2	155	—	—	100	14.3	—	—	14.3	1948
	3	122	4	—	98	16.7	20.6	—	16.5	1949
	4	105	13	—	87	19.2	20.9	—	18.9	1950
	5	63	41	33	26	23.9	25.7	23.6	21.4	1951
6	58	60	40	—	30.2	31.2	28.6	—	1952	
Big trout ♀, C Ansjön × big trout ♂, Ca Lake Vättern Cb	2	585	—	—	100	13.2	—	—	13.2	1957
	2	85	4	—	96	16.1	17.0	—	16.1	1957
	3	144	8	—	92	15.5	17.2	—	15.3	1958
	3	381	11	—	89	18.8	20.5	—	18.2	1958
Salmon ♀ × Sea trout ♂ E	3	440	2	—	98	14.8	26.0	—	14.8	1951
	4	293	7	—	93	24.8	27.9	—	24.6	1952
	5	216	22	1	67	30.5	33.8	41.0	29.4	1953
	6	55	44	22	34	34.5	39.2	42.3	32.5	1954
Sea trout ♀ × Salmon ♂ F	3	436	—	—	100	12.3	—	—	12.3	1951
	4	429	0.2	—	100	16.9	21.0	—	16.9	1952
	5	388	6	2	92	24.0	28.2	32.8	23.6	1953
	6	50	24	10	66	32.4	32.9	33.6	32.1	1954

At the age of 3 years a splitting into 3 size groups was carried out in experiment A, the groups being: 16—19 cms., 20—24 cms., and 25—33 cms. with an average length of 18.9, 21.2, and 27.9 cms., respectively. A year later the average lengths were 23.2, 27.0, and 35.8 cms., respectively. The percentages were for mature males 12.0, 11.8, and 23.5, and for mature females 1.1, 5.9, and 11.8, respectively. This agrees entirely with what has been shown to be the case in the two preceding forms of trout with respect to the importance of size for the maturity of fishes of the same age.

The degree of maturity of the salmon × trout hybrids, treated also by ALM (1955), can be seen in the Table. Also in these experiments the males reached maturity earlier than the females. The Table also shows the percentage of mature specimens to have been much greater in salmon × sea trout hybrids than in the reverse hybrids. This appears natural on account of the better growth of the former, but can also be connected with the different nature of the cross-breds.

In all these experiments with trout the average length of the mature specimens was larger for every age than that of the immature specimens as appears in greater detail from Fig. 31. Thus mature specimens were more frequent among the groups with greater than among those with smaller

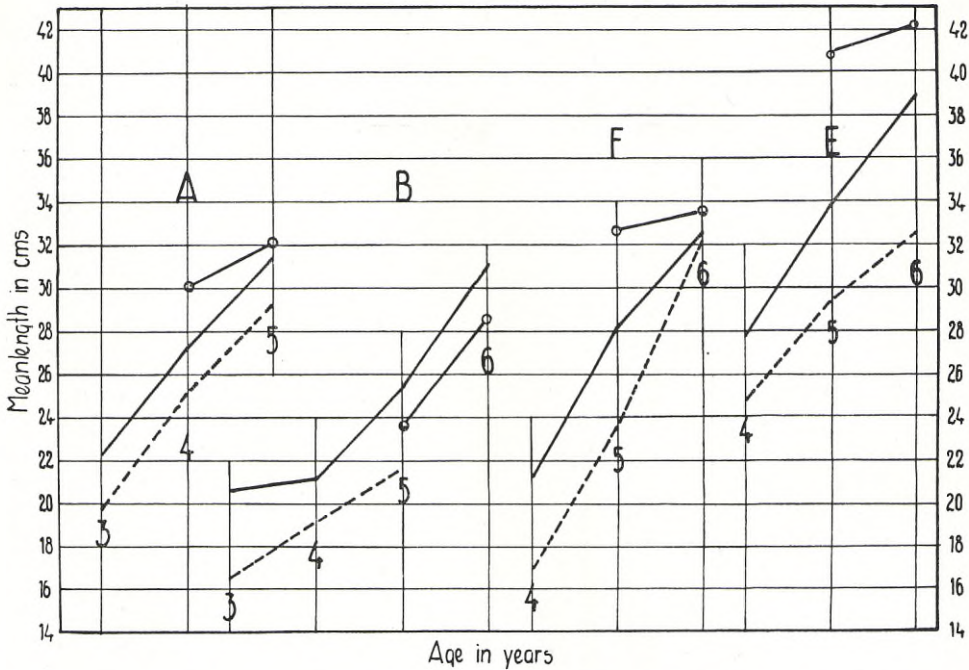


Fig. 31. Different forms of trout and hybrids. A=big trout from Switzerland, B=hybrids between small river trout ♀ and big trout ♂, F=hybrids between sea trout ♀ and salmon ♂, E=hybrids between salmon ♀ and sea trout ♂. Mean length of mature males and females and of immature specimens. ———=mature ♂, ○—○=mature ♀, - - - - - = immature specimens. The figures at the growth curves indicates the age.

length. This is corroborated by an examination of 93 specimens of big brown trout in preserved condition. Among them were found: 22 mature males with an average length of 20.5 cms., 32 immature males, average length 19.2 cms., and 39 immature females, average length 19.7 cms. In the big brown trout and the hybrids of salmon × trout the average length of the mature females was greater than that of the mature males of the same age, in the small trout hybrids, however, smaller. In this respect the hybrids between small river trout and big trout thus agree with the former, the Swiss trout and the salmon hybrids with the trout from Lake Vättern.

In the small trout hybrids the mortality was high, or 63 % in the course of 4 years. In the big Swiss trout it amounted to 48 % during 3 years. For the salmon hybrids the mortality from the 3rd to the 5th year was 51 % in one and only 11 % in the other experiment. At the age of 5 years a greater number was transferred to natural waters, and for this reason the figure at the age of 6 years can not be taken into consideration.

Table 12. *Brook trout and hybrids with char.*
Length and maturity at different ages.

Exp.	Age	Number	Percentage of number				Mean length in cm				Year of exam- min.
			Mature		Im- mat.	Total	Mature		Im- mat.		
			♂	♀			♂	♀			
Brook-trout	B	2	43	19	—	81	13.6	14.1	—	13.3	1943
	E	2	88	15	—	85	14.3	15.6	—	14.0	1945
	F	2	77	27	—	73	16.2	17.0	—	15.9	1945
	G	2	43	35	—	65	16.6	17.1	—	16.4	1945
	E+F+G	2	208	24	—	76	15.5	16.6	—	15.2	1945
	E+F+G	3	153	?	?	?	21.8	?	?	?	1946
	E+F+G	4	96	35	48	17	29.4	30.3	30.1	25.4	1947
	D	4	46	46	52	2	32.7	33.7	32.1	26.0	1941
	C	4	30	50	40	10	34.9	36.7	33.5	31.7	1941
	E+F+G	5	63	40	54	6	35.0	36.6	35.0	25.5	1948
	D	5	32	44	56	—	37.3	38.8	36.1	—	1942
C	5	13	61	39	—	41.9	43.0	40.2	—	1942	
Char × brook-trout	C	2	325	3	0.3	97	13.1	16.6	16.0	13.0	1953
	D	2	542	?	?	?	16.2	—	—	16.2	1955
	C	3	319	14	14	72	18.7	22.1	20.5	17.8	1954
	Da	3	203	20	18	62	25.8	28.6	27.9	24.2	1956
	Db	3	121	26	26	48	27.4	28.9	29.3	25.8	1956
	Ca	4	61	10	38	52	22.3	24.5	22.7	21.8	1955
	B	4	91	14	38	48	26.4	28.0	26.8	25.6	1948
	Cb	4	69	46	32	22	27.6	28.7	26.4	27.2	1955
	A	4	103	10	24	66	30.5	34.4	29.7	30.2	1948
	Da	4	225	19	31	50	31.3	34.0	30.6	30.7	1957
	Db	4	65	32	34	34	33.9	34.5	33.9	33.5	1957
	Ca	5	63	23	55	22	27.3	29.2	26.8	25.9	1956
	Cb	5	62	48	37	15	32.2	33.4	31.3	33.4	1956
	A+B	5	164	?	?	?	34.2	—	—	—	1949
	Da	5	134	24	34	42	34.6	37.8	32.4	34.6	1958
	Db	5	44	41	48	11	36.3	37.2	36.0	34.2	1958
	Ca+Cb	6	97	34	45	21	34.8	37.5	32.8	34.8	1957
	A+B	6	143	41	59	—	38.3	43.0	35.0	—	1950
	Ca+Cb	7	51	22	47	31	37.9	42.6	36.3	37.3	1958
	A+B	7	119	37	54	9	42.1	46.5	38.1	38.2	1951
(Char × Brook-trout) × brook trout	B	2	500	—	—	100	9.8	—	—	9.8	1951
	A	2	114	—	—	100	13.6	—	—	13.6	1950
	B	3	199	2	4	94	16.6	19.3	20.7	16.4	1952
	A	3	86	4	2	94	19.0	22.5	23.5	18.8	1951
	B	4	151	12	25	63	24.8	26.5	26.4	23.8	1953
	A	4	71	19	37	44	29.5	31.7	28.4	29.6	1952
	B	5	81	32	52	16	30.0	32.6	29.0	28.5	1954
	A	5	65	37	42	21	34.0	35.2	33.0	33.8	1953
	B	6	47	38	49	13	33.6	36.0	32.1	32.5	1955
	A	6	36	39	47	14	38.6	40.6	37.6	36.2	1954

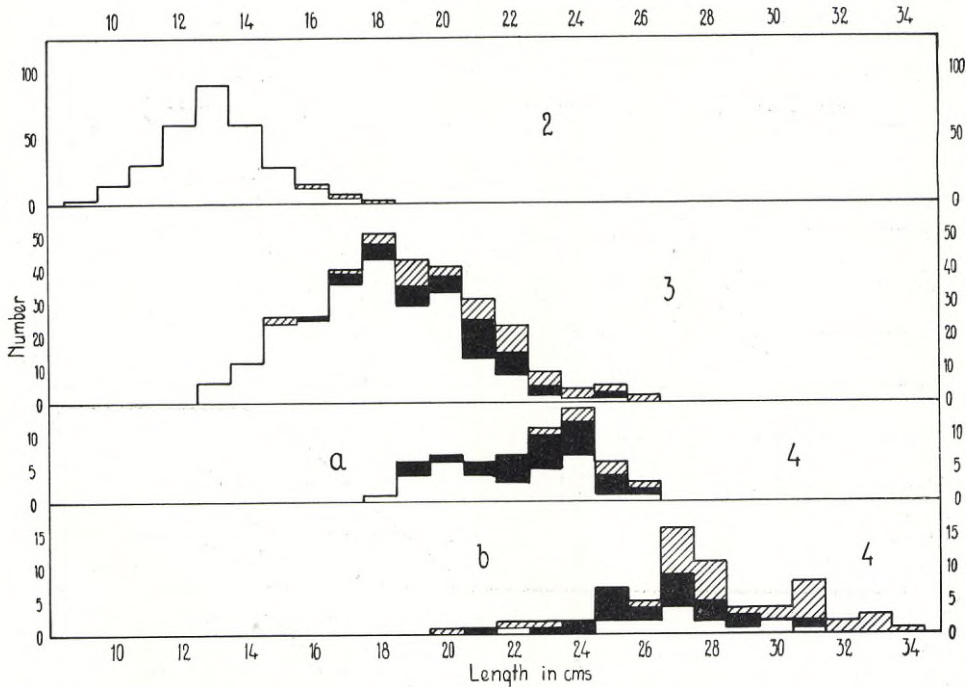


Fig. 32. Char ♀ × brook trout ♂, Exp. C. Splitting into two groups with different number in each.

4. Brook trout and hybrids with char

With brook trout and with hybrids between char and brook trout several experiments have been carried out (Table 12). On account of high mortality several of these experiments have comprised only one or a couple of years, in some cases also only a small number of specimens. Lack of ponds was the reason for the lumping together of three experiments at the age of 2 years. It must also be pointed out that it has occasionally been difficult to decide in the hybrids, especially the males, whether they were mature or not. For this reason it has been necessary in part to be guided by the colour pattern which as a rule was more pronounced in the mature specimens. It is, however, probable that the number of males, especially at higher age, has been greater than it appears from the Table.

To start with the brook trout it has to be mentioned that the percentage of mature specimens varied considerably from one experiment to the other. In the 2-year-old males it exhibited, however, a tendency towards increase with growing average length, but there existed no mature females. It seems as if the females started to reach maturity first at the age of 3 years, as is shown by the experiments with the hybrids. Unfortunately the 3-year-old

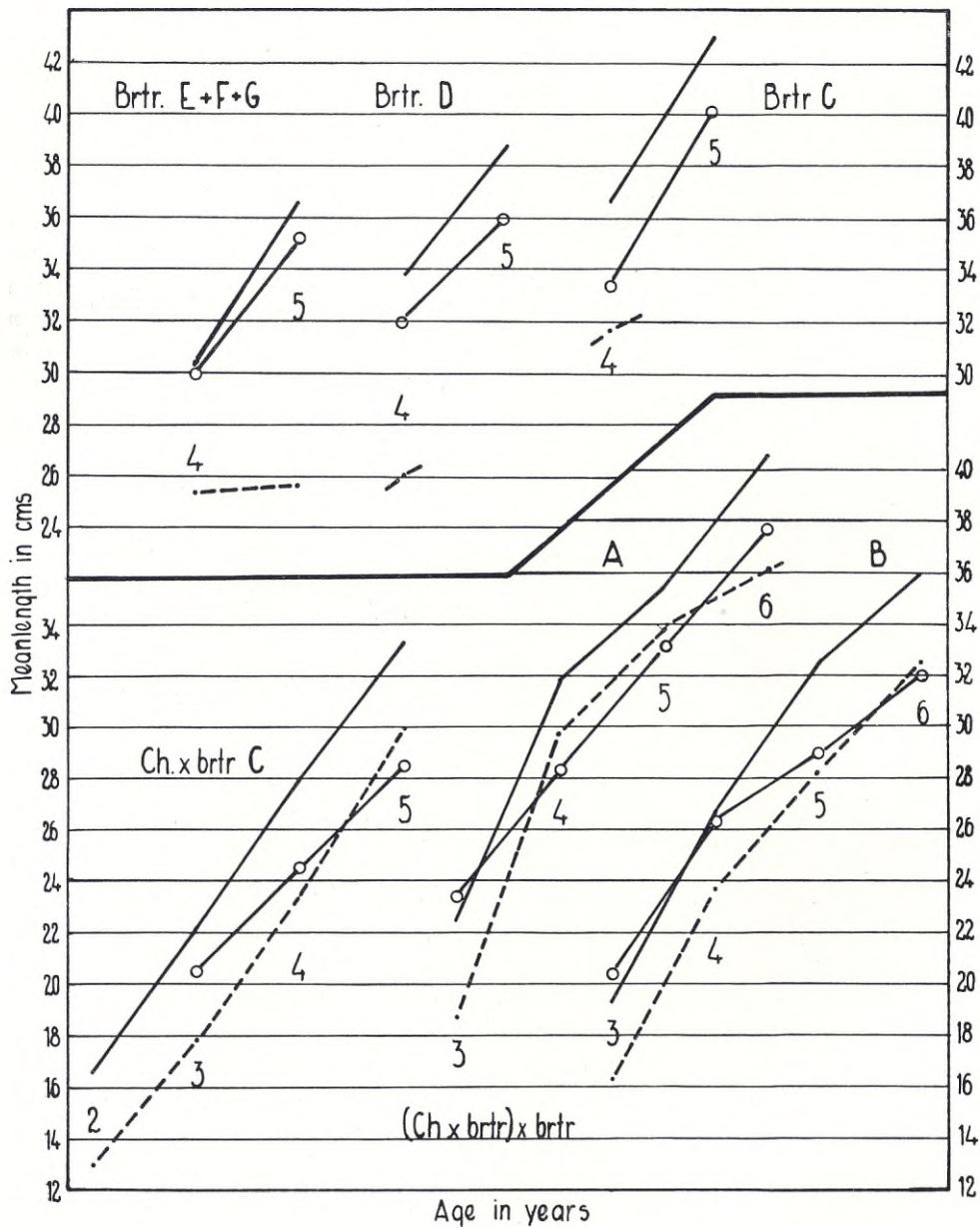


Fig. 33. Brook trout and hybrids between char ♀ and brook trout ♂, etc. Mean length of mature males and females and of immature specimens. ———=mature ♂, ○—○=mature ♀, - - - - -=immature specimens. The figures at the growth curves indicate the age.

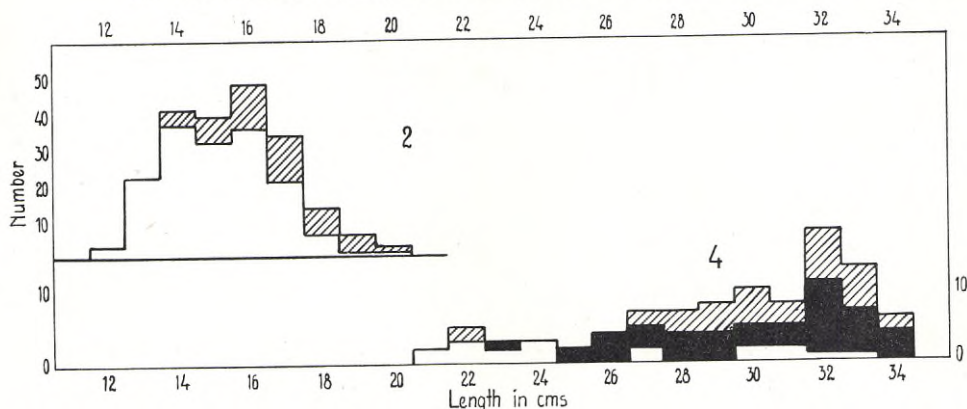


Fig. 34. Brook trout. Number of mature males and females and of immature specimens in different size groups of 2 and 4 years in exp. E+F+G.

brook trout were not examined. At the age of 2 years the experiment D with hybrids was split into two experiments Da and Db with 335 and 130 specimens of the same size in two similar ponds. This different density caused size and also percentage of mature specimens to become larger in Db than in Da. This happened at the age of 3 years, and at 4 years was still more pronounced. In experiment C with the same hybrids a splitting into two groups was carried out during the beginning of the 4th year, 97 specimens measuring 13—20 cms. forming group Ca and 96 specimens of 21—27 cms. forming group Cb. These two groups were then put into two similar ponds. The result agrees with that of the similar experiment mentioned above. At an age greater by one year the size curves coincided with each other in part (Fig. 32). The difference in average length was, however, great, and the percentage of mature males and females was higher in group Cb (Table 12). Another difference occurred in the distribution of the sexes, the percentage of males being low within group Ca, but the percentage of females higher than in group Cb. This is certainly connected with the circumstance that already at the age of 3 years the latent number of females was relatively large within the smaller group, the Table and Fig. 33 showing the average length of the males to be as a rule greater than that of the females. Apart from a few exceptions also the average length of the mature specimens surpassed at every age that of the immature ones. The conditions referred to are illustrated by Fig. 34 and by the just mentioned Fig. 32 in the same way as for the experiments with other species. In the brook trout as well as in the hybrids the number of mature specimens of the same age was greater among the groups of greater length, and also males were relatively commoner than females.

In the experiments with brook trout the different maturity groups have not been kept apart. This was, however, done in two of the experiments with

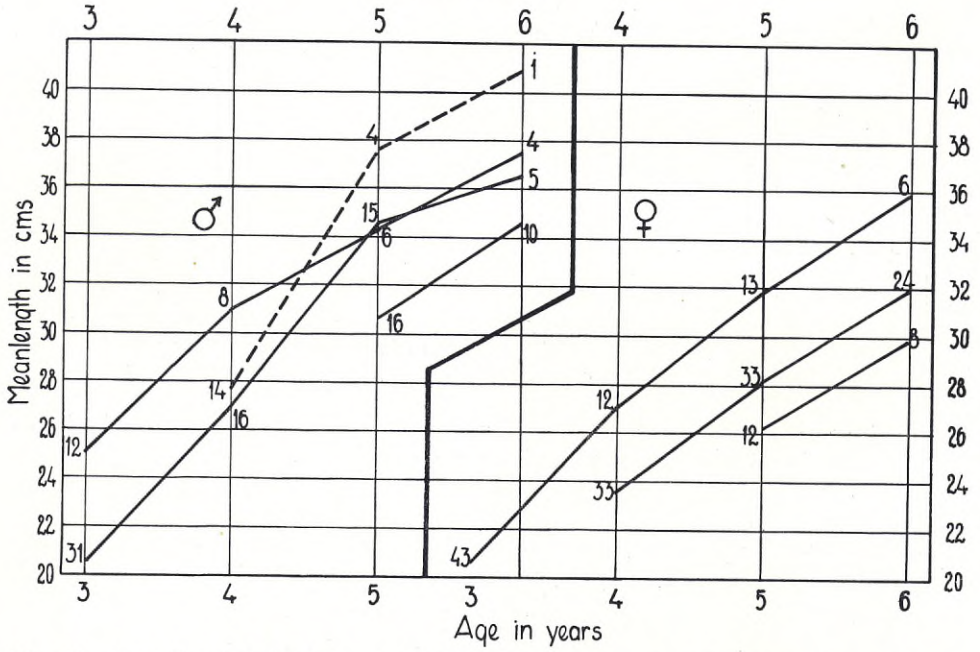


Fig. 35. Char ♀ × brook trout ♂. Relation between age at maturity and growth rate in males and females in exp. C.

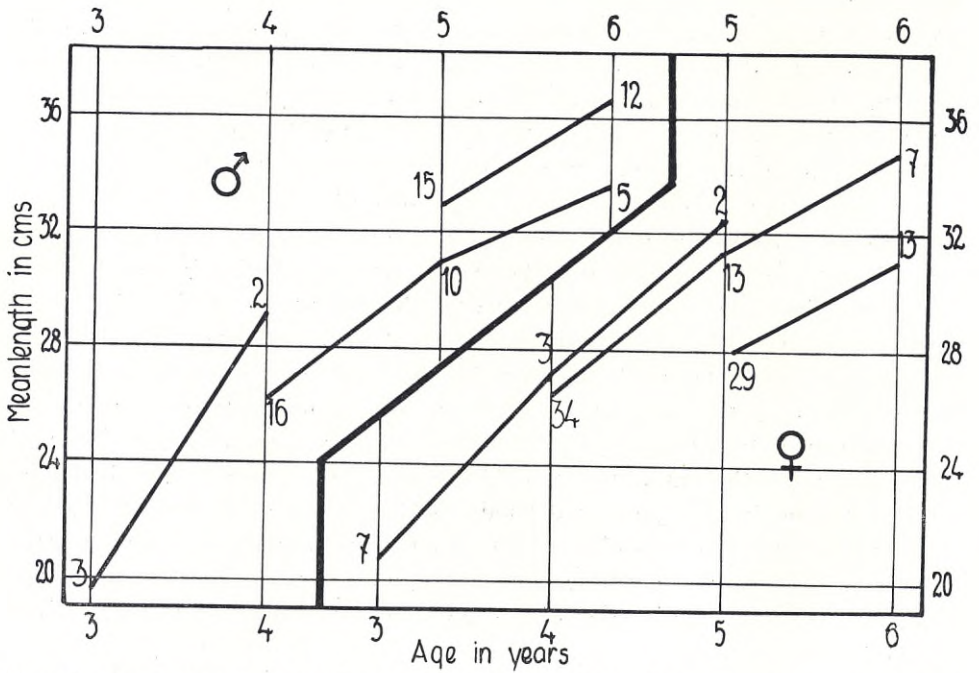


Fig. 36. (Char × brook trout) ♀ × brook trout ♂. Relation between age at maturity and growth rate in males and females in exp. B.

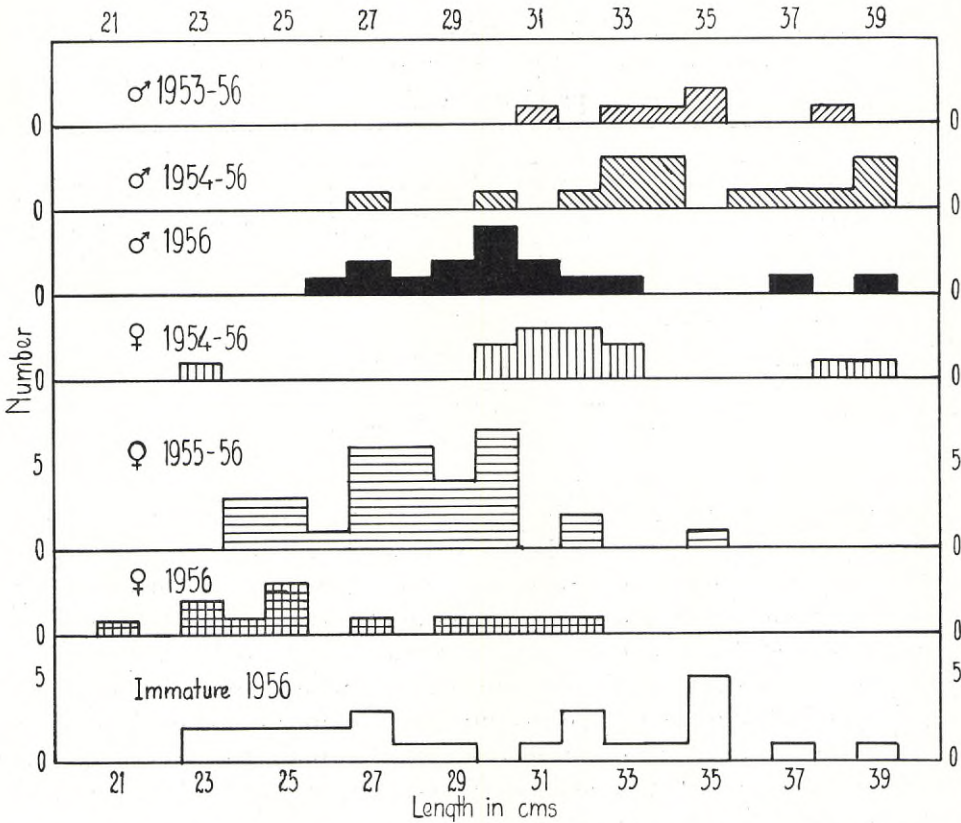


Fig. 37. Char ♀ x brook trout ♂. Number and size distribution in exp. C of males and females, matured at different ages, but all of them now 5 years old.

hybrids, the average length of these groups at increasing age being given in Figs. 35 and 36. In experiment char x brook trout, C, the specimens which were mature at the lowest age, and which were also among the biggest of their age group showed in the continuation a better growth than the specimens that had reached maturity at a greater age; this observation applies to the males for the first years, to the females all the time. Unfortunately the length of the 12 bigger 3 years old males with an average length of 25 cms., which were mature already at the age of 2 years, was not then determined. The average length of the males that were mature at the age of 4 years was somewhat greater than that of the specimens that had become mature in the previous year. In the continuation the losses were, however, so great (75 %) that the average length lost its importance. Similar remarks apply also to the experiment (char x brook trout) x brook trout B (Fig. 36). The average length of the earliest maturity group which, however, consisted of only a few specimens was greater than that of the group that reached

Table 13. *Brook trout and hybrids with char*. Mortality in the more important experiments. (Losses in different years in percentage of the number in the previous year.)

Age	Experiment							
	Brook trout C+F+G	Char ♀ × brook trout ♂		Char ♀ × brook trout ♂		Char ♀ × brook trout ♂ A+B	(Char × brook trout) ♀ × brook trout ♂ A	(Char × brook trout) ♀ × brook trout ♂ B
		Ca	Cb	Da	Db			
3	26.4	1.8		40.4		—	24.6	60.2
4	37.2	37.1	28.1	—	46.3	—	17.4	22.1
5	35.5	—	10.1	40.5	32.3	15.5	8.4	46.4
6	—	22.4		—		12.8	44.6	42.0
7	—	47.4		—		16.8	—	—
Total	69.7	84.3		67.2		38.6	68.4	90.6
Years	3	5		3		3	4	4

maturity in the following year. The average length of the males which were mature at the age of 5 years was, however, greater than that of the specimens that were at this time of the same age, but which had reached maturity already at the age of 3 and 4 years. Also at the age of 6 years these two groups exhibited the same difference in average length. With respect to the females the results agreed in both cases entirely with those from the forms of trout. Fig. 37 illustrates the distribution of the different maturity groups upon groups of length in experiment C, char × brook trout. Both the difference in size and the simultaneously great spreading of the different maturity groups is clearly evident.

With reference to Table 13 it can be pointed out that as in the experiments with trout mortality was very variable and on the whole fairly high.

Table 14. *Rainbow trout*. Length and maturity at different ages.

Exp.	Age	Num- ber	Percentage of number			Mean length in cms.			Year of exa- men.	
			Mature		Im- mat.	Total	Mature			Im- mat.
			♂	♀			♂	♀		
A	2	120	1	—	99	14.7	17.0	—	14.6	1948
a	3	45	42	—	58	18.7	18.5	—	18.8	1949
b	3	32	53	6	41	23.4	23.0	24.0	23.8	1949
c	3	24	33	17	50	27.6	27.3	28.0	27.7	1949
a—c	3	101	44	6	50	22.3	21.8	26.7	22.2	1949
a	4	43	72	28	—	27.3	26.9	27.5	—	1950
b	4	26	73	27	—	31.2	30.8	32.4	—	1950
c	4	21	52	48	—	34.7	32.2	37.2	—	1950
a—c	4	90	68	32	—	30.0	29.1	32.0	—	1950
a	6 ¹	27	81	19	—	37.4	37.4	37.2	—	1952
b	6	17	65	35	—	39.6	39.3	39.8	—	1952
c	6	13	62	38	—	43.5	43.5	43.4	—	1952
a—c	6	57	72	28	—	39.3	39.1	40.1	—	1952

¹ Not examined at 5 years.

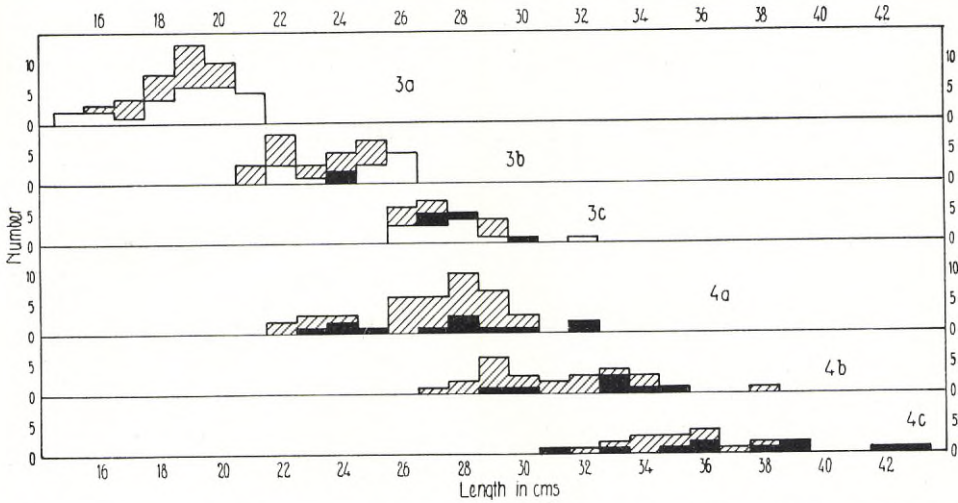


Fig. 38. Rainbow trout. Number and size distribution of mature males and females and of immature specimens of 3 and 4 years in exp. C.

This applies both to brook trout and to the hybrids. In experiment C, char × brook trout, however, the mortality was remarkably low during the third and fifth year.

5. Rainbow trout

Also with rainbow trout an experiment has been made (Table 14). At the age of 2 years only one male was mature among the biggest specimens. In the autumn of the third year the experiment was split into three size groups, viz. a, 47 specimens, 15—20 cms., b, 37 specimens, 21—25 cms., and c, 26 specimens, 26—31 cms. They were kept in the same pond. As can be seen from the Table we found in the next year, thus at the age of 3 years, an average of 44 % of males fairly uniformly distributed over the groups. There were on the other hand no mature females in the smaller group, and only few in the intermediate group. The percentage of females was on the whole remarkably low in the entire experiment. The higher percentage of females in group c, which was clearly evident among the 4-year-olds, suggests that the developing females grew better than the males already during the 3rd year. The average length of the females was mostly greater than that of the males for every age and group. As in the split experiments with other species the size curves for the three groups started at a later time partly to coincide also in this experiment. The distribution of the groups can be seen from Fig. 38. The greater length of the mature females is obvious. At the age of 4 years all specimens in the three groups were mature. As can be seen from the Table the mortality, being low at the beginning, increased later on.

Table 15. *Grayling*. Length and maturity at different ages.

Exp.	Age	Num- ber	Percentage of number			Mean length in cms.			Year of exa- min.	
			Mature		Im- mat.	Total	Mature			Im- mat.
			♂	♀			♂	♀		
A	2	250	—	—	100	14.4	—	—	14.4	1942
D	2	200	—	—	100	17.7	—	—	17.7	1950
E	2	350	—	—	100	20.1	—	—	20.1	1954
A	3	201	8	3	89	17.0	19.8	19.0	16.7	1943
D	3	172	1	1	98	19.1	21.0	25.0	19.1	1951
B	3	31	?	?	?	24.6	—	—	—	1941
Bon.	3	100	—	—	100	25.2	—	—	25.2	1956
Ea	3	183	2	5	93	26.2	29.7	26.3	26.0	1955
F	3	102	20	13	67	27.8	29.4	28.6	27.2	1955
D	4	125	5	8	87	21.8	23.1	22.4	21.7	1952
B	4	27	37	15	48	27.3	28.7	27.0	26.3	1942
Bon.	4	287	36	11	53	30.5	31.6	30.2	29.3	1957
D	5	99	13?	12?	75	24.2	25.8	25.0	23.6	1953
C	5	100	?	?	?	28.0	—	—	—	1937
B	5	24	70	30	—	31.7	32.4	30.2	—	1943
Bon.	5	129	56	12	32	34.2	34.7	33.4	33.7	1958
C	6	87	49	51	—	30.0	31.4	28.6	—	1938
D	6	32	?	?	?	31.1	—	—	—	1954

6. Grayling

In Table 15 an account of the results of experiments with grayling is given. In this Table have been included some measurements carried out on instruction at Bonäshamn hatchery, situated in the same province as Kälärne. As in the case of the hybrids char × brook trout also in the grayling the determination of the sex occasionally meets with certain difficulties. But in spite of careful examination no mature specimens could be detected at the age of 2 years. Also an examination of preserved material of the same age and with a size ranging from 15 to 19 cms. revealed exclusively immature specimens. Among grayling of 3 years isolated mature specimens of both sexes were found in some experiments, and in experiment F with the best growth a fairly large number of specimens was mature. The experiments entered into the Table under Ea and F at the age of 3 years are both descendents of the 2-year-old specimens entered under E, the latter having been split without sorting into Ea (230 specimens in one pond) and F (120 specimens in another pond). Although the fish had been of uniform size, the majority measuring 18—22 cms. at the age of 2 years, the different population density produced a difference of growth during the 3rd year as can be seen from the Table. The percentage of mature males and females was also considerably greater in group F than in group Ea. Regrettably a high mortality during the 4th year necessitated the termination of these two experiments. The connection between maturity and size is clearly seen also in the grayling of 4 and 5 years. Equally evident are the greater average length of the males in com-

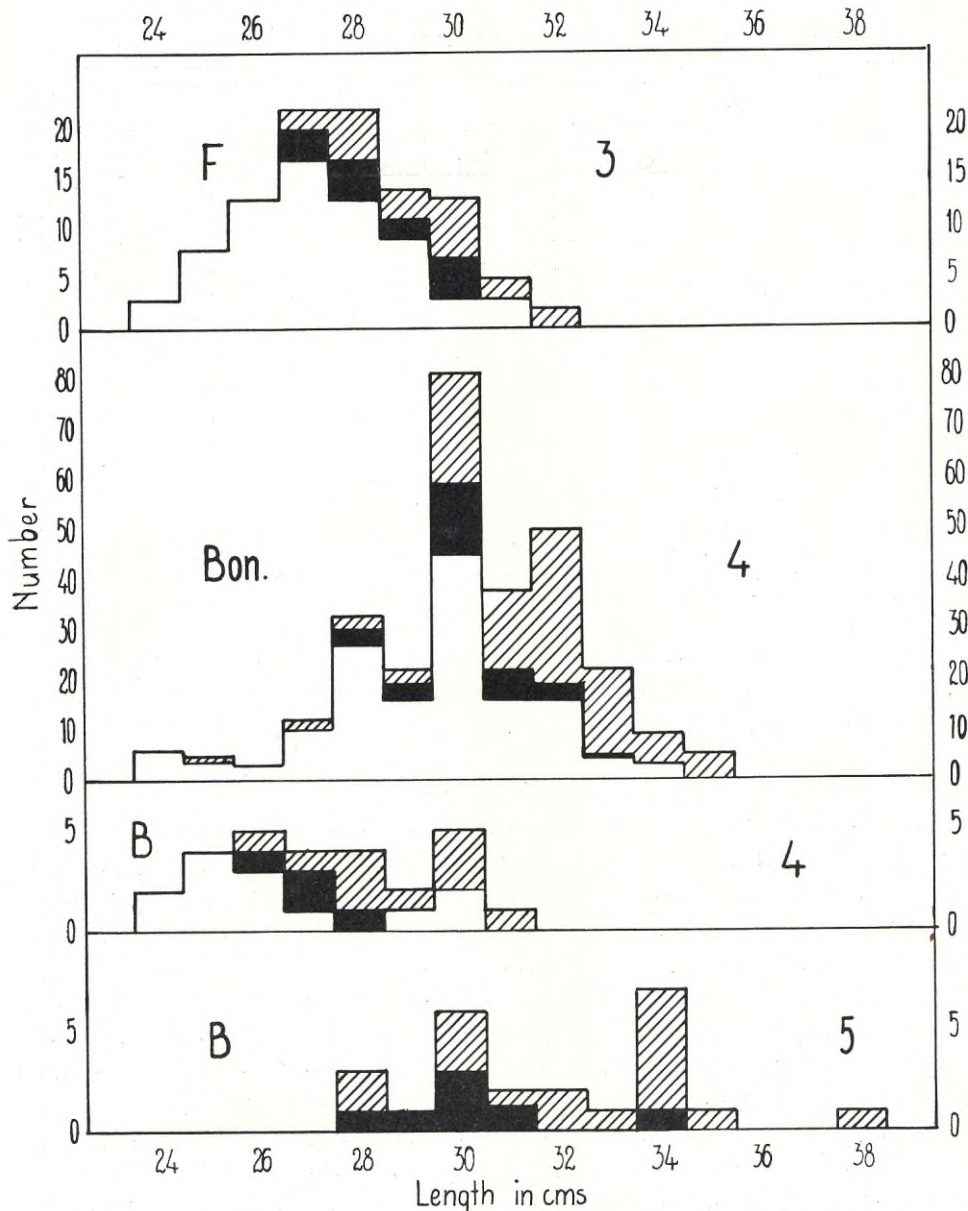


Fig. 39. Grayling. Number and size distribution of mature males and females and of immature specimens at different ages in exp. F, Bon, and B.

parison with the females and the smaller size of the immature specimens. These circumstances are evident in greater detail from Fig. 39.

The short duration of the experiments, caused by the often very great losses, prevented the following-up of the different maturity groups. For the same reason it was not possible to check during a longer time, whether or

Table 16. *Whitefish*. Length and maturity at different ages.

Exp.	Age	Num- ber	Percentage of number			Mean length in cm.			Year of exa- min.	
			Mature		Im- mat.	Total	Mature			Im- mat.
			♂	♀			♂	♀		
C ¹	2	270	—	—	100	14.3	—	—	14.3	1946
A	2	82	—	—	100	15.2	—	—	15.2	1949
B	2	180	—	—	100	21.0	—	—	—	1949
C	3	182	—	—	100	15.7	—	—	15.7	1947
A	3	53	2	—	98	17.5	?	—	17.5	1950
B	3	183	2	—	98	21.0	21.0	—	21.0	1950
C	4	172	—	—	100	18.3	—	—	18.3	1948
A	4	42	— ²	—	100	18.7	—	—	18.7	1951
B	4	124	13	2	85	21.0	22.1	21.0	21.2	1951
C	5	143	5	—	95	18.7	22.1	—	18.9	1949
A+B	5	133	7	9	84	22.7	23.4	23.8	22.5	1952
C	6	104	19	6	75	20.8	22.9	22.8	20.1	1950
C	7	76	51	24	25	24.1	24.3	23.9	23.7	1951

¹ The experiments A and B "älvsik" (*Coregonus lavaretus* L) from the mouth of the river Indalsälven, experiment C "blåsik" (*Coregonus lavaretus* × *oxyrhynchus* L) from Gimdalen, not far from Kälärne.

² The males at 3 years age must have died.

not spawning took place regularly every year, and what were the losses. It can, however, be mentioned that in some cases previously mature specimens, males as well as females, did not spawn in a succeeding year.

7. Whitefish

Table 16 contains a synopsis of three experiments with whitefish. Here it has often been difficult to decide, whether or not the fish were mature, to a great extent on account of the sensitivity to handling of the whitefish. The Table shows, however, that in experiment C from among the small-sized "blåsik" (*Coregonus lavaretus* × *oxyrhynchus*) with poor growth no males have reached maturity before the age of 5 years, and that first at the age of 7 years probably all males and half of the females were mature. In experiment B, "älvsik" (*C. lavaretus*) with the best growth on the other hand 13 % of all specimens were mature males already at the age of 4 years. Unfortunately this experiment has for some reason been lumped together with experiment A with poor growth, both experiments containing nevertheless the same species, viz. "älvsik". For this reason the maturity figures for the age of 5 years show only that here the percentage of mature specimens has been higher than in experiment C with poorer growth. From the Table and from Fig. 40 it can furthermore be seen that the average length of mature specimens exceeded that of immature specimens. The figures also suggest a greater length of the males, though the amount of material is rather too small. It has, furthermore, been established that several mature specimens did not spawn in a subsequent year. As can be seen from the Table the mortality has been rather high.

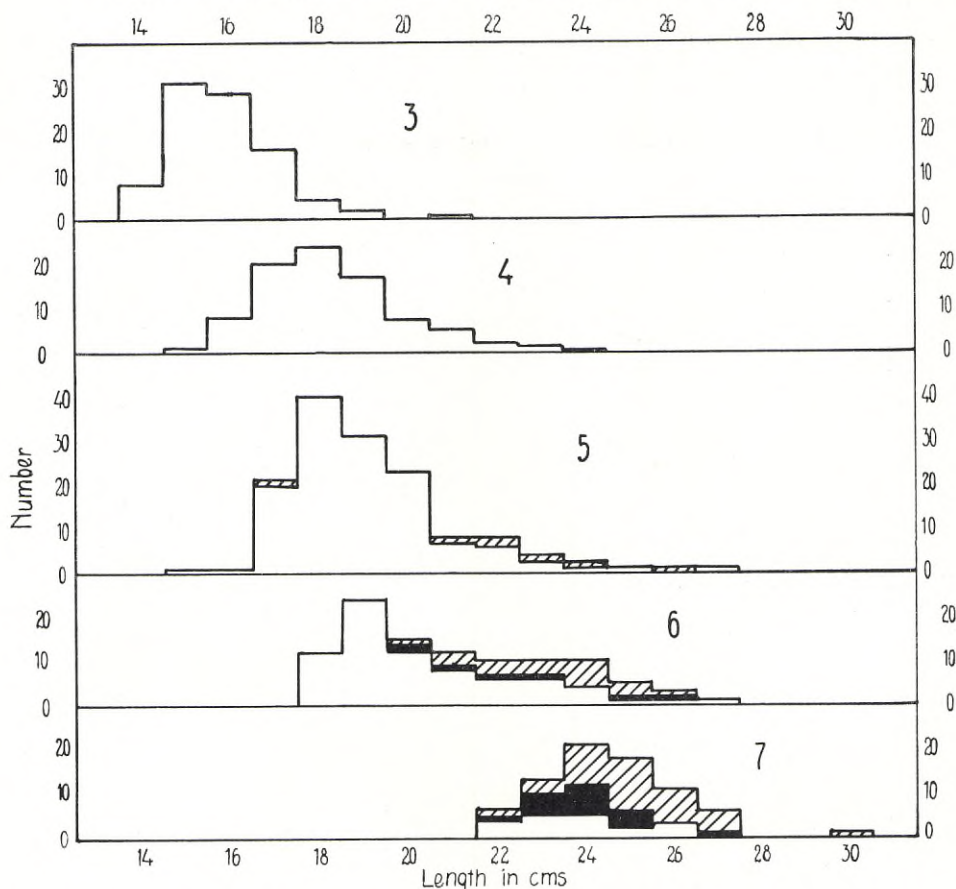


Fig. 40. Whitefish. Number and size distribution of mature males and females and of immature specimens at different ages in exp. C.

8. Perch

The perch is the species of fish which has been the object of the greatest number of experiments, both earlier and during later years. The earlier experiments being partly aimed at problems different from those in the present paper they could be used only for certain years. Other experiments again comprise a greater number of successive years.

Table 17 contains a compilation of later experimental series as well as of earlier, more sporadic experiments. The experiments A, B, C, D, E, and F (all 1949¹) are derived from roe from Lake Harsjön at Kälärne, and were at the age of one year distributed over several ponds with varying density of population. The experiments K 56 and K 57 were taken from the Lakes Hemsjön and Ansjön, both of them likewise near Kälärne, and the experi-

¹ The figures indicate the year for roe taking.

Table 17. *Perch*. Length and maturity at different ages.

Exp.	Age	Number	Percentage			Mean length in cms.				Year of examin.
			Mature		Im-mat.	Total	Mature		Im-mat.	
			♂	♀			♂	♀		
A-F 49....	1	1,900	—	—	100	3-5	—	—	3-5	1950
Hj42.....	1	1,600	—	—	100	4.0	—	—	4.0	1943
K41.....	1	1,310	—	—	100	4.3	—	—	4.3	1942
Dr43.....	1	146	4	—	96	4.5	7.7	—	4.5	1944
K37.....	1	890	—	—	100	4.6	—	—	4.6	1938
K35.....	1	3,800	—	—	100	4.7	—	—	4.7	1936
K56.....	1	1,000	—	—	100	5.8	—	—	5.8	1957
K57.....	1	97	—	—	100	6.4	—	—	6.4	1958
Hvk43.....	1	439	33	—	67	7.5	7.7	—	7.4	1944
Ävk 42-44	1	596	48	—	52	10.8	10.9	—	10.7	1943-45
Gb52.....	1	155	52	—	48	11.0	11.1	—	10.9	1953
Ga52.....	1	105	60	—	40	11.1	11.2	—	11.0	1953
Ävk54.....	1	389	54	—	46	13.4	13.3	—	13.5	1955
H49.....	2	100	—	—	100	7.6	—	—	7.6	1951
E49.....	2	100	12	—	88	8.2	8.4	—	8.1	1951
F49.....	2	592	13	—	87	8.2	8.5	—	8.0	1951
D49.....	2	825	11	—	89	8.4	8.7	—	8.3	1951
Hj42a.....	2	100	44	—	56	8.7	8.8	—	8.7	1944
K37.....	2	188	52	—	48	9.2	9.2	—	9.1	1939
K41c.....	2	175	43	—	57	9.3	9.4	—	9.2	1943
K56a.....	2	134	7	—	93	9.7	10.9	—	9.6	1958
C49.....	2	108	4	—	96	9.7	10.0	—	9.6	1951
K41a.....	2	202	41	—	59	10.2	10.4	—	10.1	1943
K57a.....	2	74	30	—	70	10.5	10.7	—	10.4	1958
K41b.....	2	127	47	—	53	11.0	11.1	—	10.9	1943
B49.....	2	74	43	—	57	11.4	11.4	—	11.4	1951
A49.....	2	42	38	—	62	11.7	12.2	—	11.4	1951
K56b.....	2	43	28	—	72	12.0	12.8	—	11.7	1958
K41d.....	2	59	50	—	50	12.5	12.4	—	12.6	1943
K56c.....	2	60	47	—	53	13.2	13.1	—	13.2	1958
Gb52.....	2	140	54	—	46	13.2	13.2	—	13.2	1954
Dr43.....	2	47	58	23	19	13.9	13.6	14.7	13.9	1945
Ga52.....	2	91	63	35	2	18.5	18.2	18.8	19.0	1954
D1 49.....	3	95	51	—	49	10.3	10.5	—	10.2	1952
F49.....	3	800	46	—	54	10.9	10.9	—	10.8	1952
E49.....	3	49	35	—	65	11.6	11.7	—	11.5	1952
D2 49.....	3	103	41	—	59	12.1	12.2	—	12.1	1952
K35c.....	3	140	48	21	31	12.2	11.8	14.3	11.4	1938
C49.....	3	71	45	—	55	12.6	12.5	—	12.7	1952
K41a.....	3	242	41	—	59	12.8	12.6	—	13.0	1943
K41c.....	3	57	44	—	56	13.3	13.2	—	13.4	1943
K35a.....	3	52	58	27	15	13.6	13.4	14.0	13.9	1938
K41b.....	3	100	38	4	58	13.9	13.6	15.5	14.1	1944
K37.....	3	141	46	16	38	14.0	13.6	15.3	14.0	1940
A49.....	3	35	52	—	48	14.1	13.8	—	14.7	1952
Gb52.....	3	63	59	2	39	14.9	14.5	15.0	15.4	1955
K35b.....	3	55	36	24	40	15.0	14.4	15.2	15.4	1938
B49.....	3	54	52	2	46	15.3	15.1	15.0	15.6	1952
K35d.....	3	27	37	63	0	17.7	16.2	18.6	—	1938
Ga52.....	3	60	58	40	2	19.3	18.8	20.1	20.0	1955
F49.....	4	682	49	—	51	11.5	11.4	—	11.6	1953
D1 49.....	4	92	57	12	31	14.1	13.9	14.5	14.0	1953
K35x.....	4	286	52	26	22	15.3	14.7	16.8	15.0	1939
K41a.....	4	143	55	36	9	15.4	14.9	16.5	13.9	1945

(Continued)

(Continued)

Exp.	Age	Number	Percentage			Mean length in cms.				Year of examin.
			Mature		Im-mat.	Total	Mature		Im-mat.	
			♂	♀			♂	♀		
C49	4	34	50	15	35	15.7	15.3	16.6	15.6	1953
E49	4	27	49	19	32	15.9	15.5	16.4	15.9	1953
K35c	4	76	50	38	12	16.6	15.9	17.6	16.0	1939
D2 49	4	76	40	55	5	16.8	16.0	17.3	16.7	1953
B49	4	28	50	39	11	17.0	16.7	17.6	16.0	1953
K35a+b+d	4	136	43	57	0	19.1	18.0	19.8	19.1	1939
Ga52	4	38	66	34	0	20.8	20.3	21.5	—	1956
K37	4	110	46	54	0	20.8	19.6	22.1	—	1941
F49	5	402	51	21	28	13.5	13.5	16.8	13.3	1954
D1 49	5	75	64	33	3	17.4	16.9	18.3	18.0	1954
Fa49	5	83	54	46	0	18.7	18.3	19.3	—	1954
L49	5	56	50	48	2	18.5	17.6	19.4	18.0	1954
K49	5	116	41	59	0	20.1	19.1	20.7	—	1954
Ga52	5	36	67	33	0	21.3	20.5	22.1	—	1957
K35x	5	240	?	?	0	21.7	?	?	—	1940
F49	6	274	45	35	20	16.9	16.1	18.8	15.4	1955
D1 49	6	78	64	28	8	19.2	18.4	20.7	20.3	1955
L49	6	48	48	50	2	19.8	19.1	20.4	20.0	1955
K49	6	103	44	56	0	20.5	19.6	21.3	—	1955
K35x	6	203	46	54	0	21.1	20.8	21.4	—	1941
Ga52	6	36	69	31	0	23.9	23.7	25.1	—	1958
F49	7	158	51	42	7	19.1	17.9	20.8	16.9	1956
D1 49	7	52	65	35	0	20.3	19.5	21.8	—	1956
K49	7	92	45	55	0	20.8	19.9	21.7	—	1956
L49	7	45	47	51	2	21.7	21.2	22.3	21.0	1956
K35x	7	190	43	57	0	23.2	22.6	23.5	—	1942
Ga52	7	34	71	29	0	23.8	23.3	25.1	—	1959
F49	8	117	56	49	5	20.9	19.3	22.9	18.5	1957
K49	8	88	42	58	0	21.5	20.4	22.5	—	1957
D1 49	8	28	61	39	0	21.7	20.6	23.5	—	1957
L49	8	44	48	50	2	23.1	21.7	24.4	23.0	1957
K35x	8	160	50	50	0	24.5	23.5	25.3	—	1943
F49	9	113	54	41	5	22.3	20.6	24.7	20.3	1957 ¹
K49	9	78	44	56	0	22.4	21.3	23.3	—	1957
D1+L49	9	64	56	44	0	23.3	22.0	25.0	—	1957
K35x	9	153	44	56	0	26.1	24.8	27.1	—	1944 ²
D1+L+K49	10	45	73	27	0	22.8	22.3	24.2	—	1959
K35x	10	41	46	54	0	25.6	24.0	27.0	—	1945
K35x	11	37	51	49	0	26.4	—	—	—	1946
K35x	12	31	48	52	0	27.3	25.5	29.1	—	1947
K35x	13	28	61	39	0	28.1	—	—	—	1948
K35x	14	27	?	?	0	28.5	—	—	—	1949
K35x	15	16	?	?	0	27.9	—	—	—	1950
K35x	16	15	60	40	0	28.9	26.7	32.2	—	1951
K35x	17	13	62	38	0	29.0	—	—	—	1952
K35x	18	9	56	44	0	—	—	—	—	1953
K35x	19	8	50	50	0	31.4	27.5	33.2	—	1954
K35x	20	8	50	50	0	31.7	29.5	33.8	—	1955
K35x	21	9	?	?	0	—	27.0—37.0	—	—	1956

¹ Investigated in the autumn.

² High mortality in the winter 1944/45.

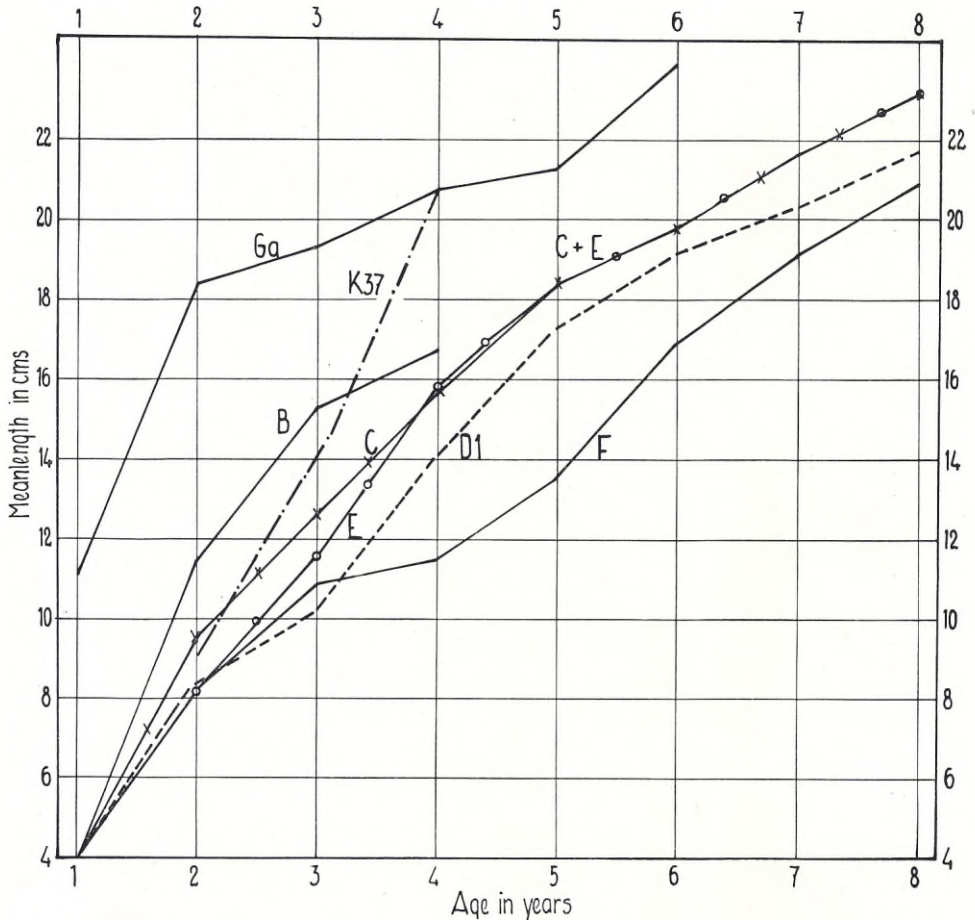


Fig. 41. Perch. Rate of growth in the most important experiments.

ments K 35 and K 37 from stunted populations in the small Kälarne lake Aborrtjärn 2. The experiment K 41 consisted of offspring from perches in ponds at Kälarne. Experiment Hj 42 was taken from Lake Hjälmaren, and experiment Hvk 43 from a small lake near Uppsala. The experiments Ga and Gb 52 were derived from Hyttödammen near Älvkarleby Hatchery (River Dalälven), and were at the age of one year distributed in different numbers over different ponds. From the same pond come the experiments Ävk 42—44, Ävk 54 and Dr 43.

The following remarks have to be added. At the beginning of the third summer from the experim. D two groups, viz. D1 with 97 small specimens of 9—10.4 cms. and D2 with 110 big specimens of 11.6—17 cms., were separated for new experiments. Simultaneously 420 medium-sized specimens were transferred from the same experiment D to experiment F of approxi-

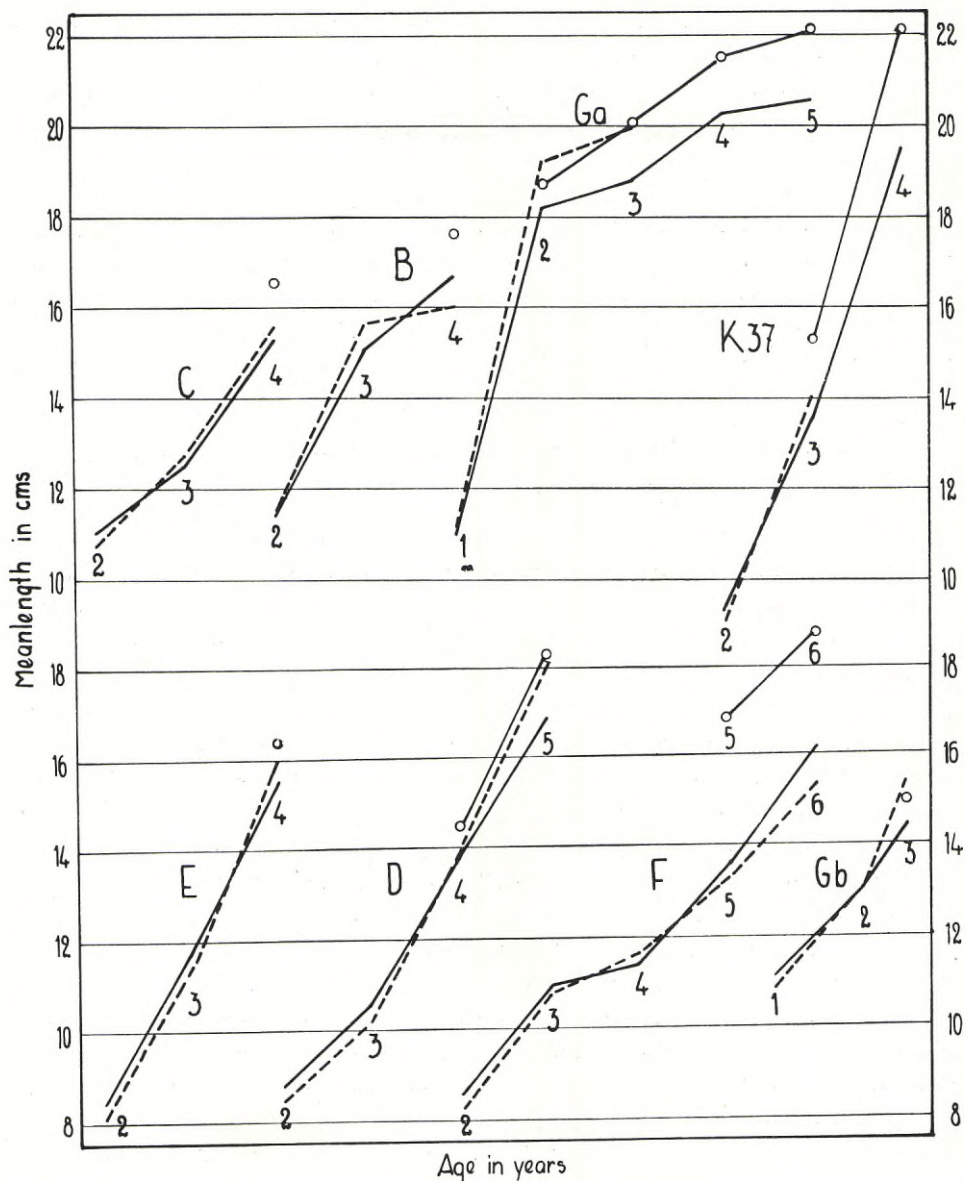


Fig. 42. Perch. Mean length of mature males and females and of immature specimens. ———=mature ♂, ○—○=mature ♀, ·····=immature specimens. The figures at the growth curves indicate the age.

mately the same size. From this latter experiment 100 specimens 4 years old and of the size which was normal within the experiment were removed, and brought under more favourable conditions which led to better growth (Fa). This experiment was terminated at the age of 5 years. On account of similar

size the experiments D2 and B together with 18 specimens from a smaller experiment were lumped together at the age of 4 years, and formed a continued experiment K 49. For the same reason the experiments C and E were lumped together into experiment L 49. Also later some fusions were carried out, as can be seen from the Table.

In Fig. 41 we have drawn the growth curves for the experiments which on account of different density of population exhibited noticeable differences in growth and average size. There special attention is called to experiment Ga with an unusually good growth all the time, and experiment F, where on the contrary growth was very poor. The other experiments occupy an intermediate position.

*The length of mature and immature specimens of the same age
within a certain experiment*

Table 17 and Fig. 42 give the average length and, indirectly, the growth rate of males and females with increasing age. In the experiments, where mature males were present at the age of one year, their length surpassed that of the immature specimens. Only in experiment Ävk 54 with the greatest average length the opposite was the case. At the age of two years the mature males were still bigger than the other specimens in all experiments with poorer, and in several experiments with better growth. In some experiments of this type the average length of the males was on the contrary somewhat smaller than that of the immature specimens. In the two experiments in which also mature females were found the average length both of these and of the immature specimens exceeded that of the males. In the slow-growing experiments the average length of the mature males was also at the age of three years greater than that of the immature specimens, the contrary being the case in experiments with better growth. In the experiments in which mature females were found these were bigger than the males. In some experiments these mature females were also of greater average length than the immature specimens, in other experiments they were smaller. With the exception of a couple of experiments the average length at the age of 4 years was greatest for the females and smallest for the males, the immature specimens occupying an intermediate position. At higher age the average length of the females often surpassed that of the males by several centimetres. This obviously results in a considerable difference in weight between the sexes.

Figs. 43—45 show the distribution of mature males and females and of immature specimens over groups of different length with increasing age. Here the amplitude of variation is much narrower than in the species of fish dealt with previously. The mentioned difference in size between the sexes is, however, very evident.

The above shows the following. During the first or the first and second

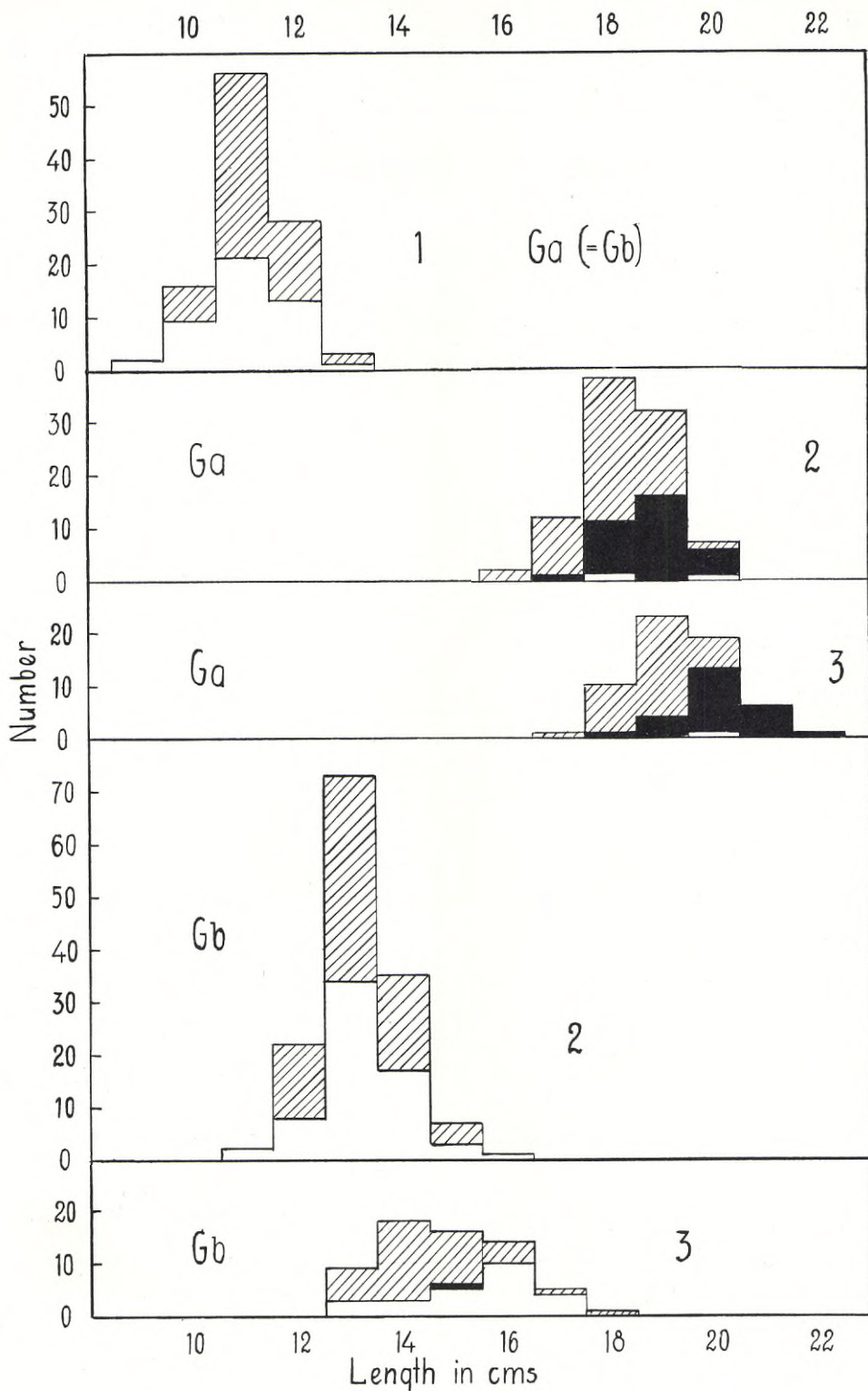


Fig. 43.

Figs. 43—45. Perch. Number of mature males and females and of immature specimens in different size groups at different ages in a fast-, a medium-, and a slow-growing experiment. Fig. 43 exp. Ga, Gb, Fig. 44 — exp. C+E (L), Fig. 45 — exp. F, Fa.

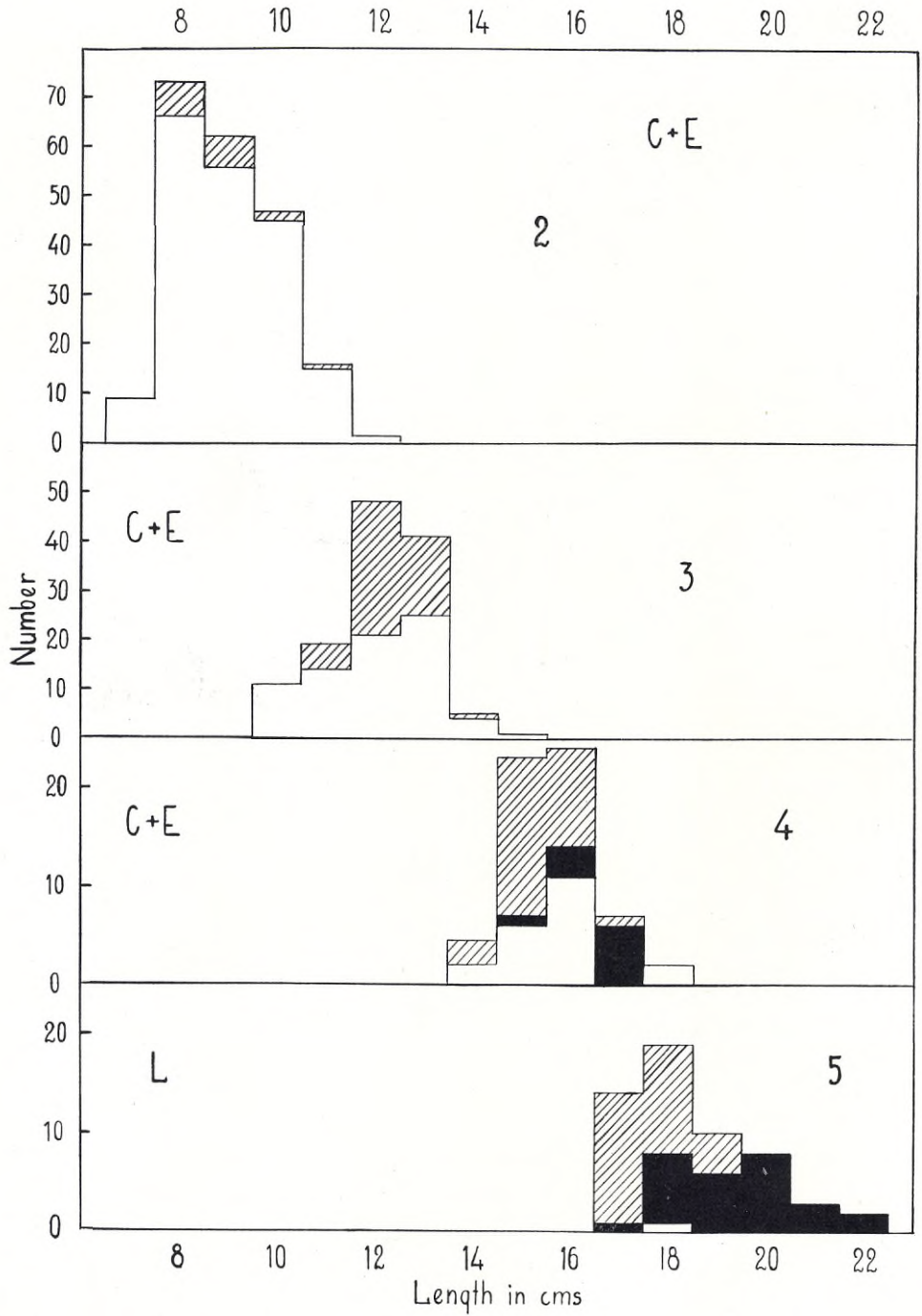


Fig. 44.

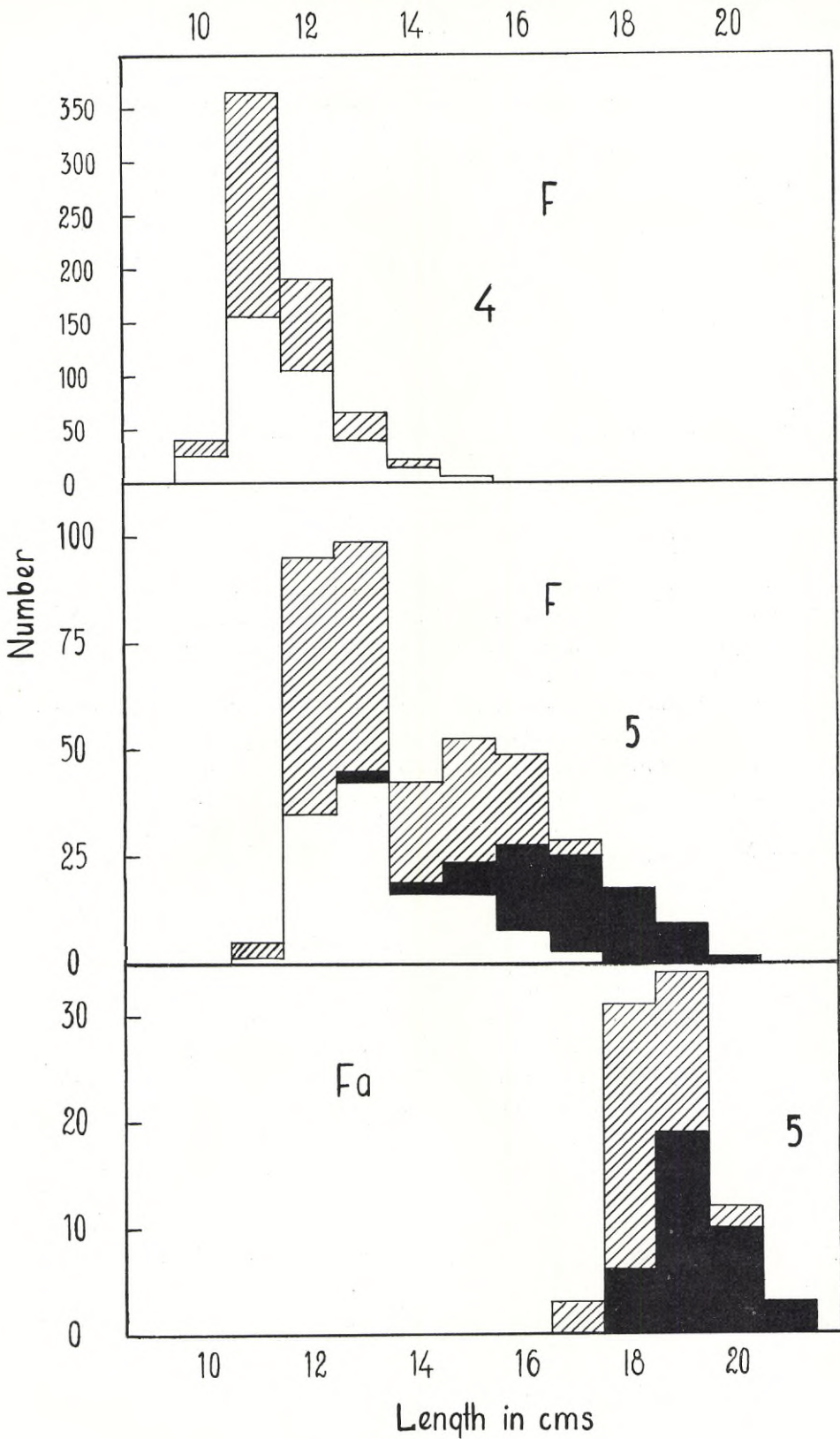


Fig. 45.

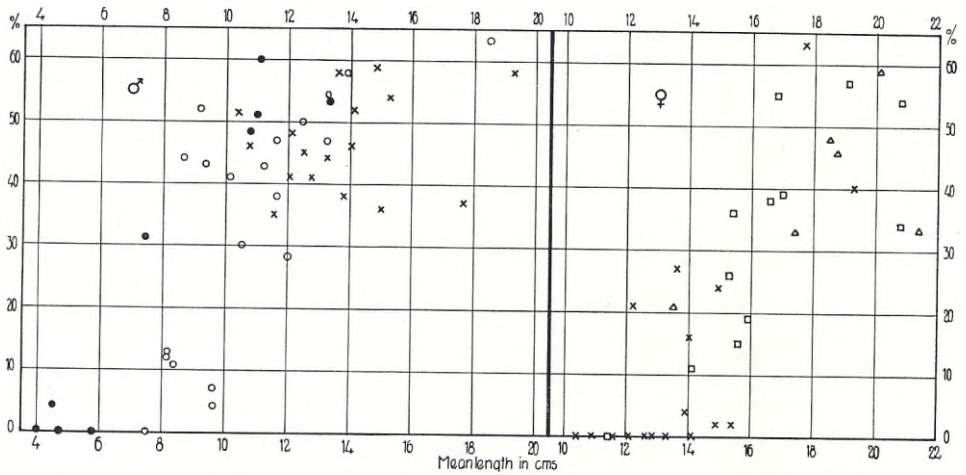


Fig. 46. Perch. Relation between mean length, age, and maturity. ●=1, ○=2, ×=3, □=4, △=5 years old.

year the growth of the males exceeds that of the still not mature females. Also during the third year the males have a distinct lead in growth in experiments in which the growth has been fairly poor and the average length rather small. In the majority of cases, however, the other specimens have grown better than the males. This holds good either they were still all immature or had in part reached maturity. On account of the now reigning abundance of mature males the immature specimens must at all events be constituted mainly of females. Starting from the second or at least the third year the growth of the latter is better than that of the males. This is still more pronounced in the continuation.

The number of mature specimens of the same age in experiments with better and poorer growth (=year classes with different growth)

Fig. 46 shows the relation between the percentage of mature specimens and the average length and age for all specimens in the experiment. It covers the entire material entered into Table 17. As in the species of fishes dealt with above we have found also here, in spite of several deviations, a higher percentage of mature specimens in the experiments with better growth than in those with poorer growth but of the same age. The Table and the diagram show furthermore that in experiments with good growth a great part of the males reached maturity already at the age of one year. In experiments with poorer growth the maturity of the males was, with the exception of certain experiments, low, in experiment H with the poorest growth=0. The majority of the males was, however, now mature. In 3-year-old specimens the percentage of mature males varied between 35 and 58 %, and it appears probable that practically all males were then mature.

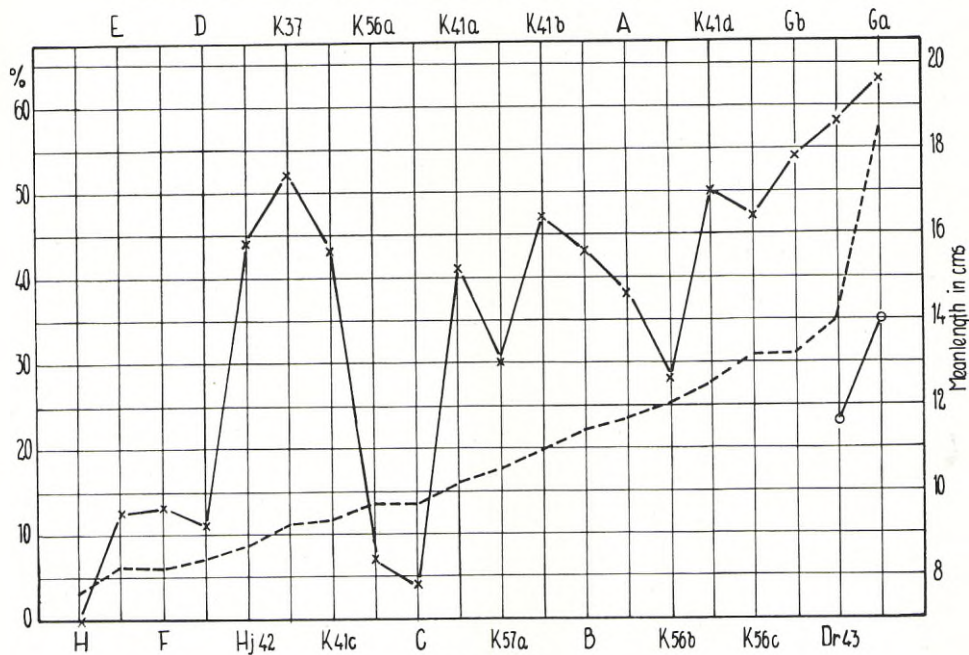


Fig. 47 a.

Fig. 47. Perch. Percentage of mature males and females in experiments with a) 2, b) 3, and c) 4 years old specimens. $\times-\times-\times = \text{♂}$, $o-o-o = \text{♀}$, -----= mean length in the experiments.

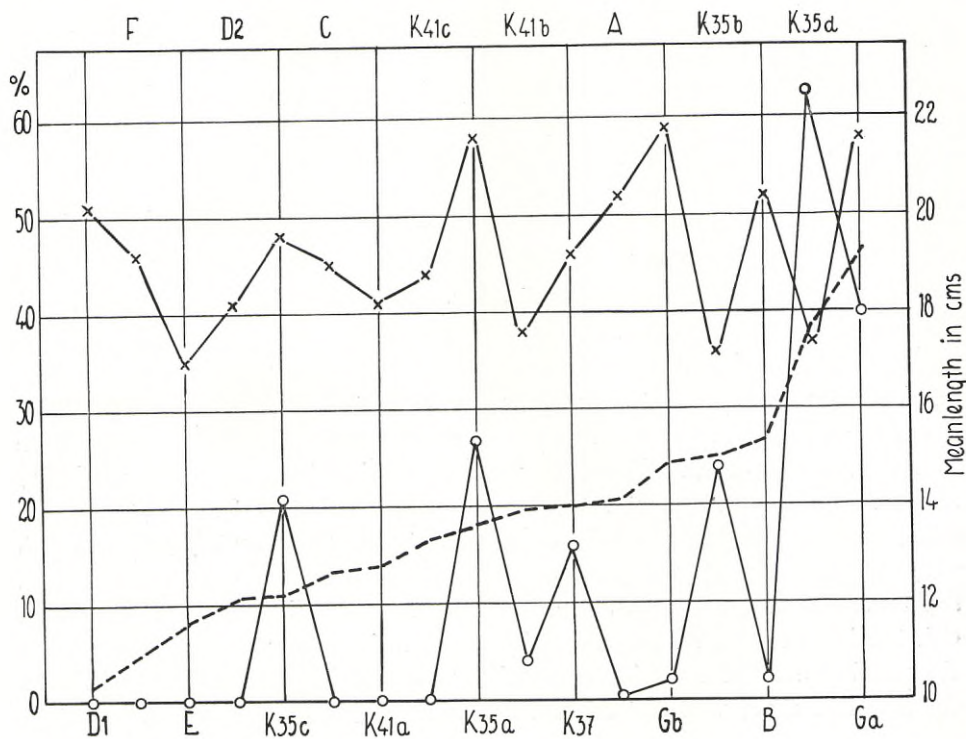


Fig. 47 b.

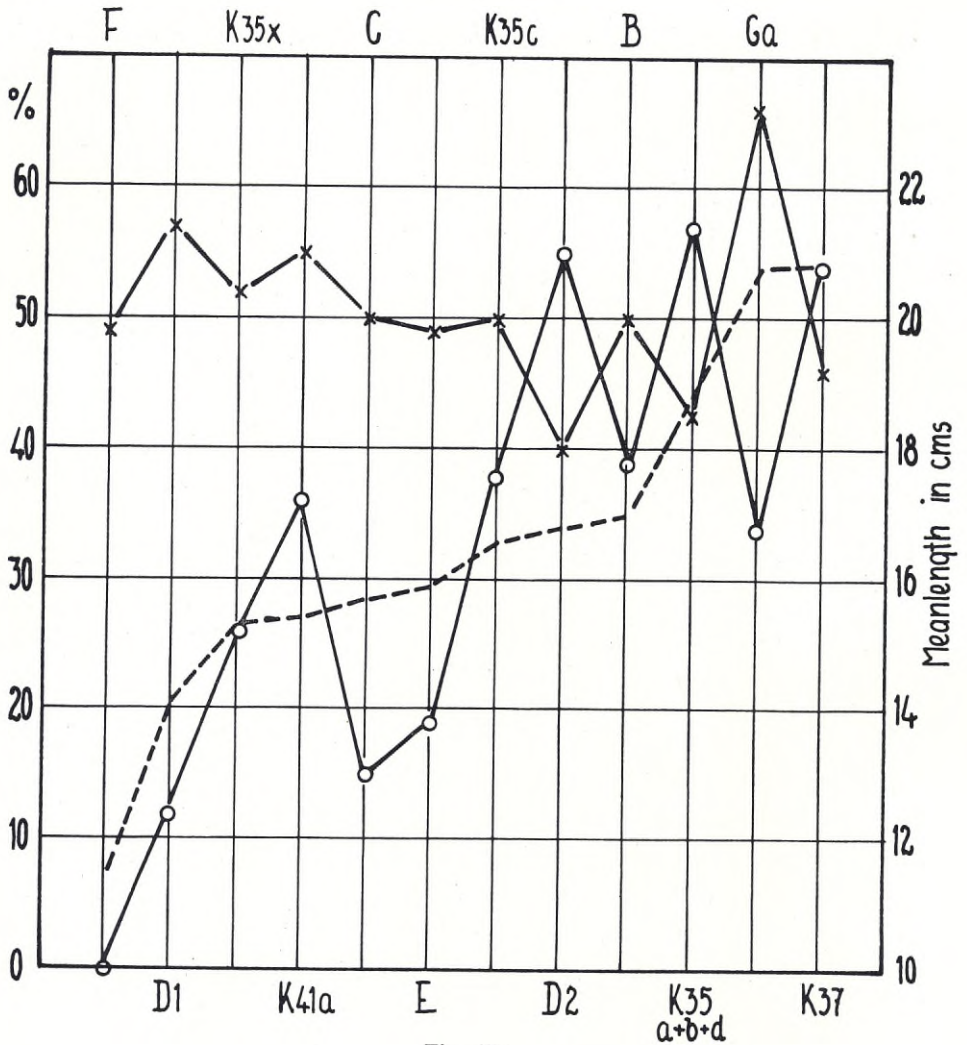


Fig. 47 c.

In exceptional cases, but only in the experiments with the best growth rate, maturity of females appeared already at the age of 2 years. In the two experiments with especially good growth rate, viz. K35d and Ga, practically all females were mature at the age of 3 years. Great variation in the percentage of maturity was found in experiments with moderately good growth rate. In the more poorly growing experiments no females were as yet mature. The maturity of the females of 4 years was seen to increase on the whole with the increasing average length in the experiments. Mature females were still missing only in experiment F with an exceptionally poor growth rate. At the age of 5 years at last a greater number of females was still immature

Table 18. *Perch*. Number and percentage of mature males and females at different ages.

Age	Mature				Immature	
	♂		♀		Number	%
	Number	%	Number	%		
1	768	6.2	—	—	11,659	93.8
2	865	26.4	42	1.0	2,374	72.6
3	943	44.0	127	5.9	1,074	50.1
4	854	49.4	446	25.8	428	24.8
5	393	51.2	253	33.0	122	15.8
6	362	48.6	313	38.9	67	9.0
7	282	49.0	278	49.1	11	1.9
8	220	50.5	210	46.9	7	1.6
9	198	48.5	204	50.0	6	1.5

in this experiment, whereas otherwise practically all specimens had now attained maturity. A comparison between Figs. 43 and 44 for perch of two years and of Figs. 44 and 45 for those of 4 and 5 years gives a clear idea of the connection between maturity and size. In order to throw additional light on it we have represented in Fig. 45 the distribution of size of the specimens (Fa) which at the age of 4 years had been removed from experiment F, and placed during the fifth year under more favourable conditions, but which at the age of 4 years had been of the same size. On account of the increased growth all specimens had here reached maturity, whereas in the main experiment with continued poor growth 28 % of the 402 specimens had still not reached maturity. Fig. 43 shows that in the same way experiment Gb on account of its lagging behind in growth in comparison with experiment Ga is far behind the latter in maturity.

As in the previous cases we give also for the perch in Fig. 47 a graphic representation of the percentages of mature males and females in experiments with increasing average length in the different experiments. Particularly striking are here the high percentage of 2-year-old mature males in the experiments Hj42, K37, and K41c, and the low percentage of such males in the experiments K56A and C. In the same way the percentage of mature females among 3-year-old specimens is remarkably high in experiments K35c and K35a, but low in the experiments C, K41a, K41c, A, and Gb. These deviations will be treated in greater detail on p. 112. A striking feature was also the high percentage of males in experiment Ga, while experiment K35d was completely dominated by the females. Also experiment D1 exhibited a high percentage of males, while conditions were the opposite in D2. This might possibly depend on the sorting according to size of the 2-year-old specimens in experiment D. Table 18 contains a synopsis of the whole material with regard to maturity at different ages. From this it can be seen that during the later years, when all males and the majority of the females are mature, the sex ratio is on the whole 1 : 1.

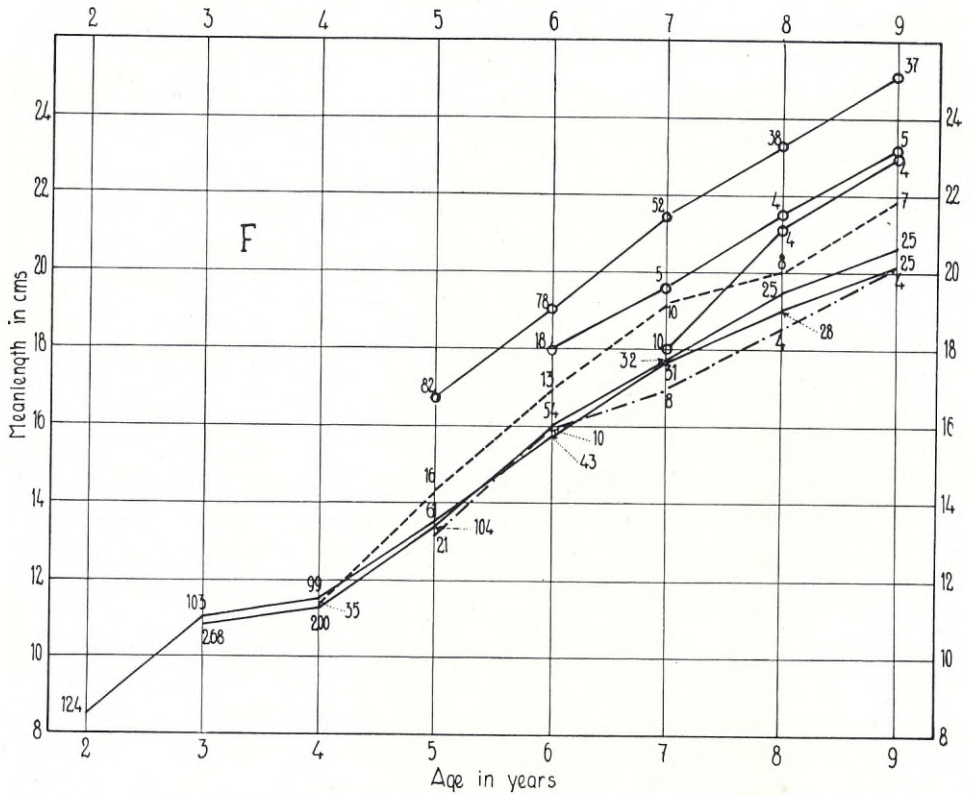


Fig. 48. Perch. Relation between age at maturity and growth rate in males and females in exp. F. ——— = ♂, ○—○ = ♀.

Growth and length within the different maturity groups

In the same way as it has been done in the experiments with the forms of trout the different maturity groups have been kept apart also in several experiments with perch, but on account of the generally poor growth rate in perch and of the often fairly great losses the results are not as clear as for the trout.

In experiment F (Fig. 48) two larger groups of mature males could be followed right up to the age of 9 years. Here the average length of the males which had reached maturity earliest, viz. at the age of 2 years, remained during the following three years higher than the average length of the males that became mature one year later, i.e. at the age of 3 years. At the age of 6 years on the contrary the average length of this group somewhat exceeded that of the former, at 7 years it equalled it, in order to be slightly greater again at the age of 8 and 9 years. A third group of males, 35 specimens, became mature at the age of 4 years, and at that time was intermediate in

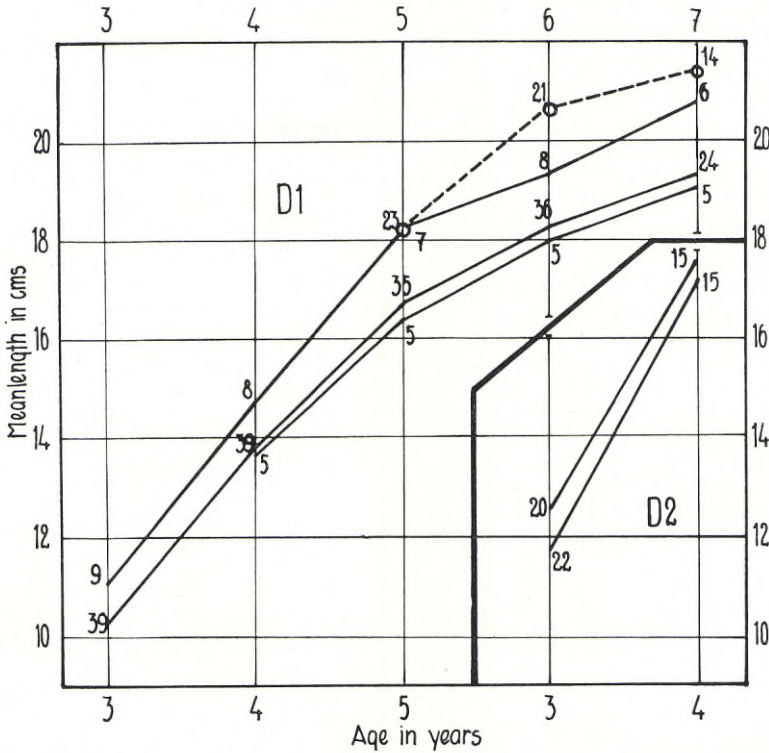


Fig. 49. Perch. Relation between age at maturity and growth rate in males and females in exp. D1 and D2. — = ♂, ---○ = ♀.

size between the two earlier groups in order to surpass them considerably in the continuation. At the age of 5 years another 21 males became mature the average length of which remained somewhat below that of the groups that had matured earlier, this relation continuing also during some of the following years.

The three maturity groups of the females exhibited all the time a greater average length of the earlier matured group. Comparison with what has been said above about the average length these results show, in spite of the mentioned deviations, that the conditions are the same here as for the trout, viz. that the specimens that have reached maturity in a certain year were usually among those which then had a better growth. The results show likewise that the specimens which have become mature at a lower age continued also later on to exhibit a better growth than the specimens that had reached maturity at a later date. This is particularly obvious in the females with their better growth rate.

The same result is shown by the Figs. 49 and 50. In experiment D1 the course of the curves of average length for the three male maturity groups is all the time such that the earlier mature males have an advance over the

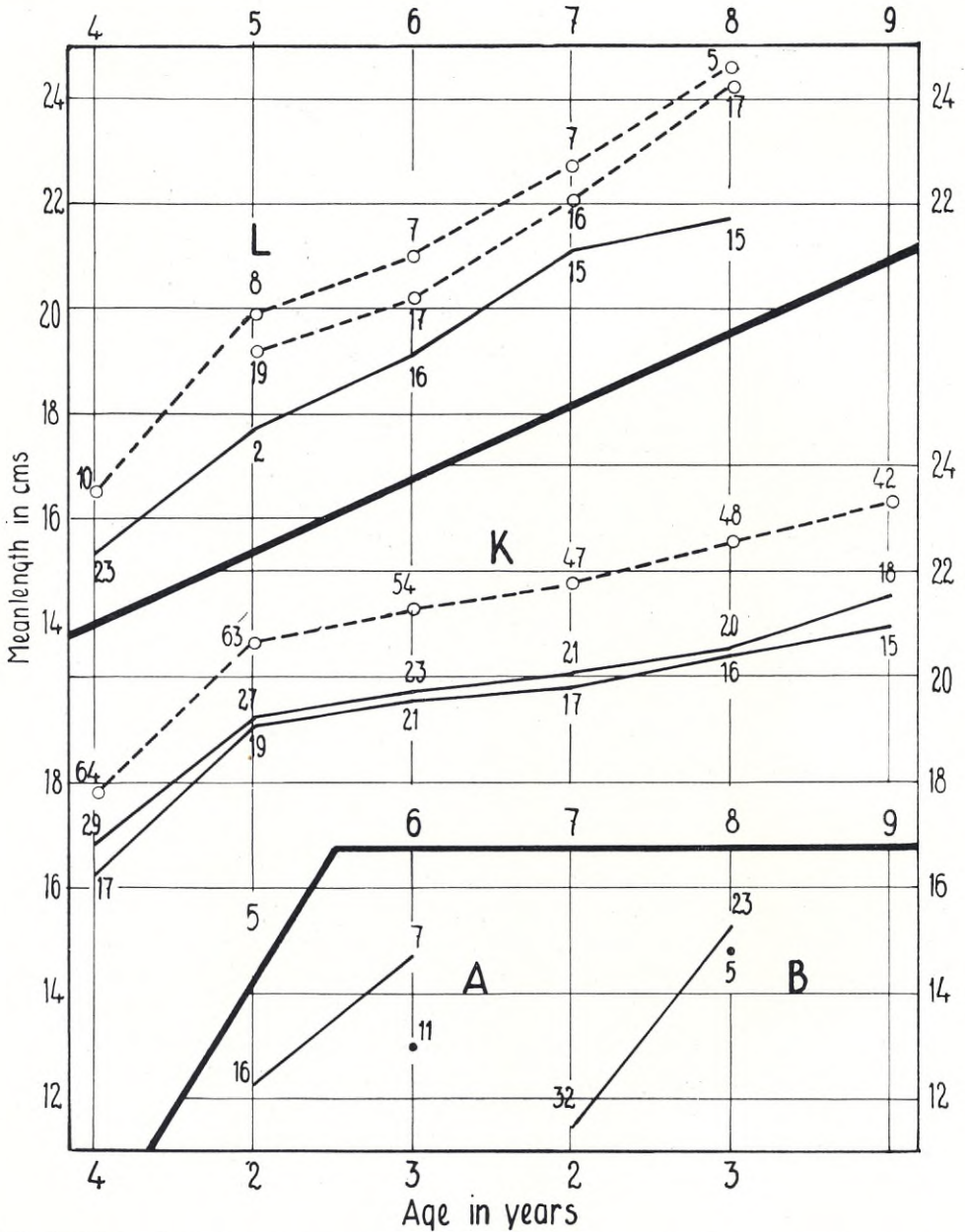


Table 19. *Perch*. Mortality in the more important experiments. (Losses in different years in percentage of the number in the previous year.)

Age	Experiments															Age
	Ga	K35	Gb	A	B	C	D	E	F	K37	D1	L	K	D2	Average	
2	13.3	—	9.7	—	—	—	8.4	—	—	—	—	—	—	—	10.5	2
3	34.0	—	55.0	16.7	27.0	34.3	—	51.0	—	25.0	—	—	—	—	34.7	3
4	36.7	—	—	—	48.1	52.1	—	45.0	14.8	22.0	3.2	—	—	26.2	31.1	4
5	5.3	16.8	—	—	—	—	—	—	41.2	—	18.5	8.2	5.2	—	15.6	5
6	0	15.0	—	—	—	—	—	—	31.8	—	0	16.7	11.2	—	14.6	6
7	5.6	6.4	—	—	—	—	—	—	42.3	—	33.3	6.3	10.7	—	17.6	7
8	—	15.8	—	—	—	—	—	—	26.0	—	46.2	2.2	4.3	—	19.5	8
9	—	4.4	—	—	—	—	—	—	3.4	—	—	11.1	11.4	—	7.6	9
10	—	—	—	—	—	—	—	—	—	—	—	6.7	—	—	6.7	10
Total	67.6	44.1	59.1	—	62.2	68.5	—	73.0	86.1	41.5	72.8	21.4	24.2	—		
Years	6	5	2	—	2	2	—	2	6	2	5	4	5	—		

proves nothing. On account of the heavy losses during the 8th year the groups have not been followed up beyond the 7th year. The sizes of the maturity groups in the experiments K and L in which the losses were rather small show the same tendency as those in the experiments F and D1. In experiment K two groups of males which had become mature at different ages could be followed up. Of these the earlier had an advance over the later during all successive years. The experiment L comprised only one group of males, but two of females. To them apply the same remarks as to the male groups in experiment K. The experiment Ga comprised strictly speaking only one maturity group of each sex. Apart from these there existed only some isolated specimens which attained maturity later. On this account no comparison between different groups is possible. The same applies to experiment Gb. On the other hand we have entered into the diagrams the figures available from the experiments A, B, and D2. All of them cover admittedly only two years and a small number of individuals, but their results agree with those obtained in the preceding experiments. Everything thus indicates that the specimens which reach maturity in a certain year are found mainly among those which have enjoyed the best growth. Fig. 51 shows the size distribution of the different maturity groups for experiment F. It appears from it that the spreading within the different groups is admittedly rather wide. For groups consisting of a relatively great number of specimens it exhibits, however, a more or less binominal distribution of size.

Annual or omitted spawning

It seems as if in general the perch spawned every year, though lack of time did not permit in all cases to determine, whether or not earlier mature

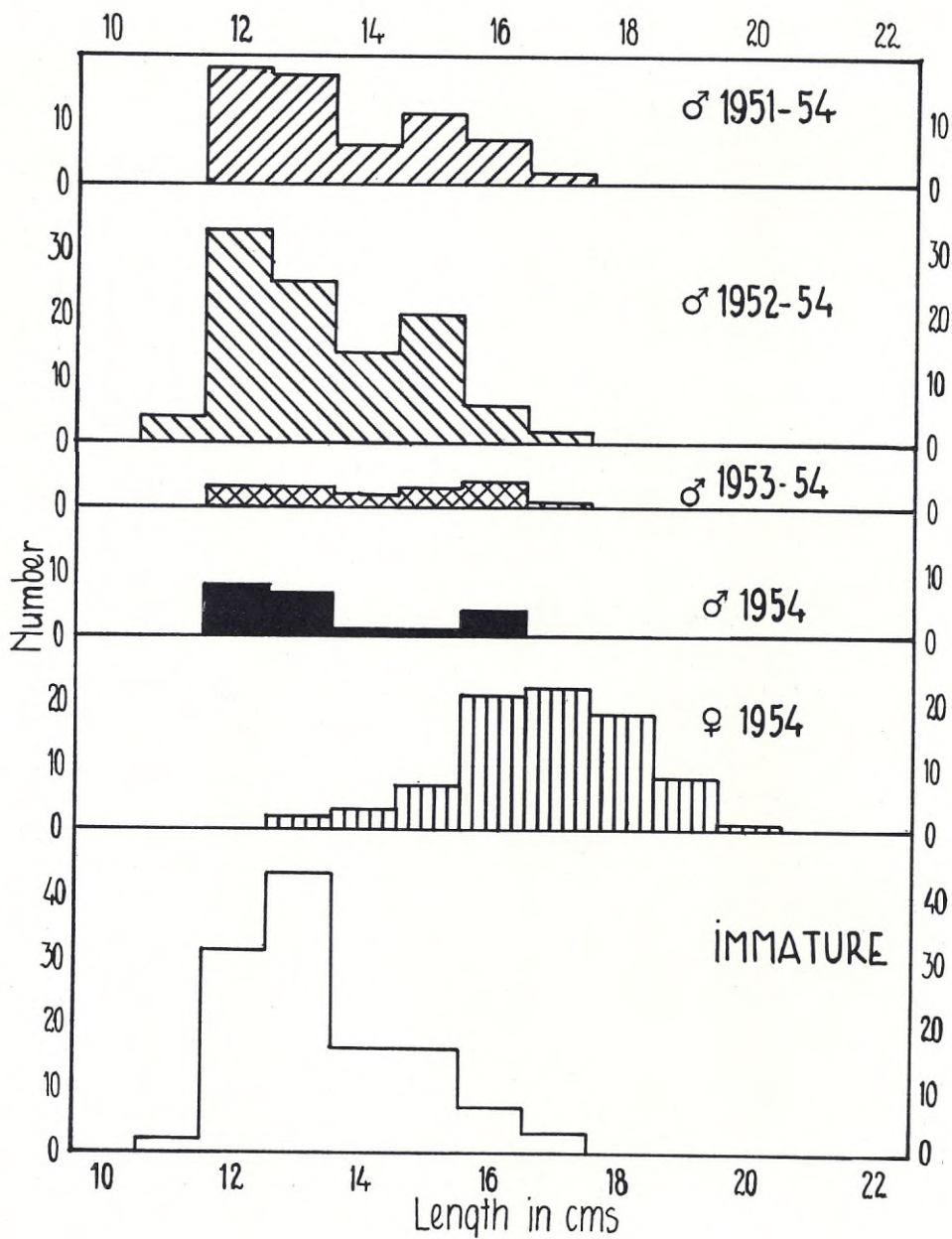


Fig. 51 a.

Fig. 51. Perch. Number and size distribution in exp. F of males and females, matured at different ages, but all of them now a) = 3, b) = 5 years old.

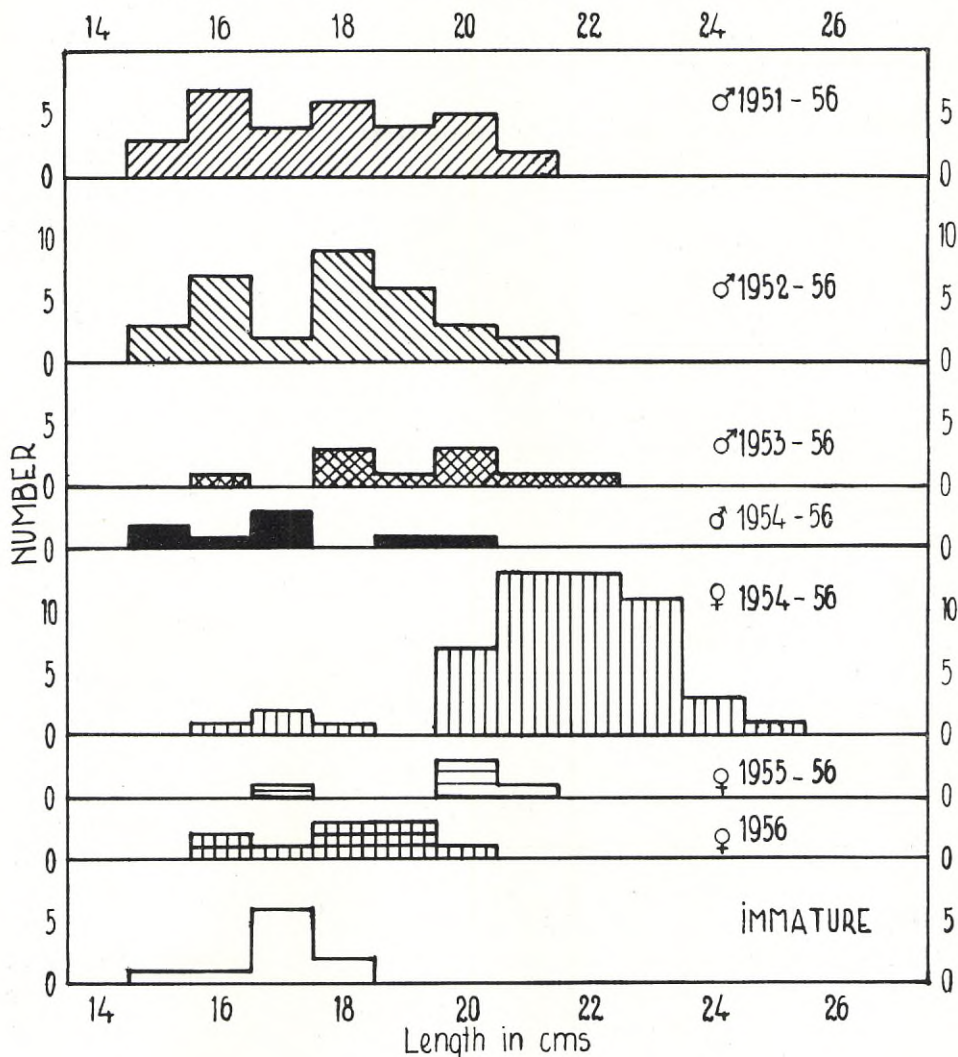


Fig. 51 b.

specimens had again been spawning. In the majority of cases such a check has, however, been effected. This control showed that in the preponderating number of experiments all earlier mature specimens, male as well as female, had again been spawning. In isolated instances this has nevertheless not been the case. Thus in one experiment 7 specimens from among 42 previously mature females did not spawn again, and in another experiment the corresponding figure was 2 out of 63. In one case 6 out of 18 previously mature males did not spawn again. These examples constitute, however, exceptional cases.

Table 20. *Perch*. Mortality in different maturity-groups. (Losses at termination of the experiment in percentage of the number at maturity.)

Experiments	Age at maturity	Number of				Mortality in. %		Number of years between maturity and termination
		♂		♀		♂	♀	
		Maturity	Termination	Maturity	Termination			
F	2	124	25	—	—	79.8	—	7
	3	268	25	—	—	90.7	—	6
	4	35	7	—	—	80.0	—	5
	5	21	4	82	37	80.9	54.9	4
	6	—	—	18	5	—	72.2	3
	7	—	—	10	4	—	60.0	2
D1	2	30	6	—	—	80.0	—	5
	3	39	24	—	—	38.5	—	4
	4	5	5	11	2	—	81.8	3
	5	—	—	23	14	—	39.1	2
Ga	1	61	24	—	—	60.6	—	6
	2	—	—	32	10	—	68.8	5
K	2	125	18	—	—	85.6	—	7
	3	30	15	—	—	50.0	—	6
	4	—	—	64	42	—	34.4	5
L	2	16	3	—	—	81.3	—	6
	3	45	15	—	—	33.3	—	5
	4	—	—	10	5	—	50.0	4
	5	—	—	19	17	—	10.5	3

Mortality

Following the principles applied to the above treated species the percentages for the mortality during different years have been entered into Table 19. The figures show a strong variation, and in some cases the losses are considerable. In some experiments they have, however, been rather insignificant at higher ages. In the experiment F with the poorest growth rate they have been high all the time with the exception of a single year. The average for the entire material exceeds the mortality figures for the small and the big forms of trout.

Table 20 shows the mortality for the different maturity groups in some of the experiments covered by Figs. 48—50. In some cases these figures show a decreasing mortality in the groups that had reached maturity at a higher age. This result is, however, quite natural, since the number of years from the maturity to the termination of the experiment decreases at the same time. In experiment F with the largest number of specimens we found about the same mortality for different groups. This is synonymous with a higher mortality in the later maturity groups. In certain cases the mortality of the males has been slightly higher than that of the females. This can in part be explained by the smaller number of years comprised in the figures of losses for the females.

In order to get a clearer idea about the mortality in males and females the figures for five experiments (F, K, D1, L, K35x) continued to a age of 9 years have been chosen. On account of the circumstance that, as is shown in Table 17, practically all males ought to have reached maturity at the age of 4 years this figure has been chosen for starting value. At the age of 4 years the five included experiments contained 705 males and 692 females and immature specimens. At the age of 9 years the corresponding figures were 198 and 210. Correspondingly the percentage of losses was somewhat higher for the males than for the females, viz. 71.9 and 69.6 %, respectively. These figures do, however, not express a strikingly greater mortality in the males. In experiment K35x which was continued to a high age the number of specimens dropped considerably towards the termination (Table 17), yet the sex ratio remained fairly constant throughout. Mention must, however, be made of an experiment which exhibited diminution in the number of males. This refers to the transfer in the year 1934 of 50 specimens from a stunted population to a pond for further breeding. The average length was 14.2 cms. Probably about 60 % were males. In the year 1944 only 13 specimens were found, in the year 1954 only two males and four females, and in the year 1956 one male of 35 cms. and three females of 27, 29, and 38 cms., respectively. At their transfer to the pond these perch probably were 4 or 5 years old. Thus in 1956 the total age was 27 or 28 years.

9. Roach

With the intention of examining the above treated problems also for some species of the family Cyprinidae roe of roach has been procured on several occasions, and the fry been reared in ponds with varying density of population. The mortality was, however, very high already in the course of the first or the first few years. For this reason no continued series of experiments with a greater number of specimens could be obtained. The results of two experiments have nevertheless been included, and entered into Table 21. The different density of the population produced differences of growth right from the beginning. In neither case has maturity been established in specimens of 1 or 2 years. Not before the age of 3 years did some males reach maturity. Although the material was now very small, the percentage of mature specimens in the experiment with better growth was nevertheless twice as high as in the other experiment, where the average length of all specimens was 2.5 cms. smaller. This becomes evident also from Fig. 52 which at the same time shows the distribution of the size classes. The average length of the mature males was in either case smaller than that of the immature specimens. This condition continued in experiment M1, where with rising age the difference became more pronounced. In this experiment the females did not reach maturity before the age of 6 years (4 specimens),

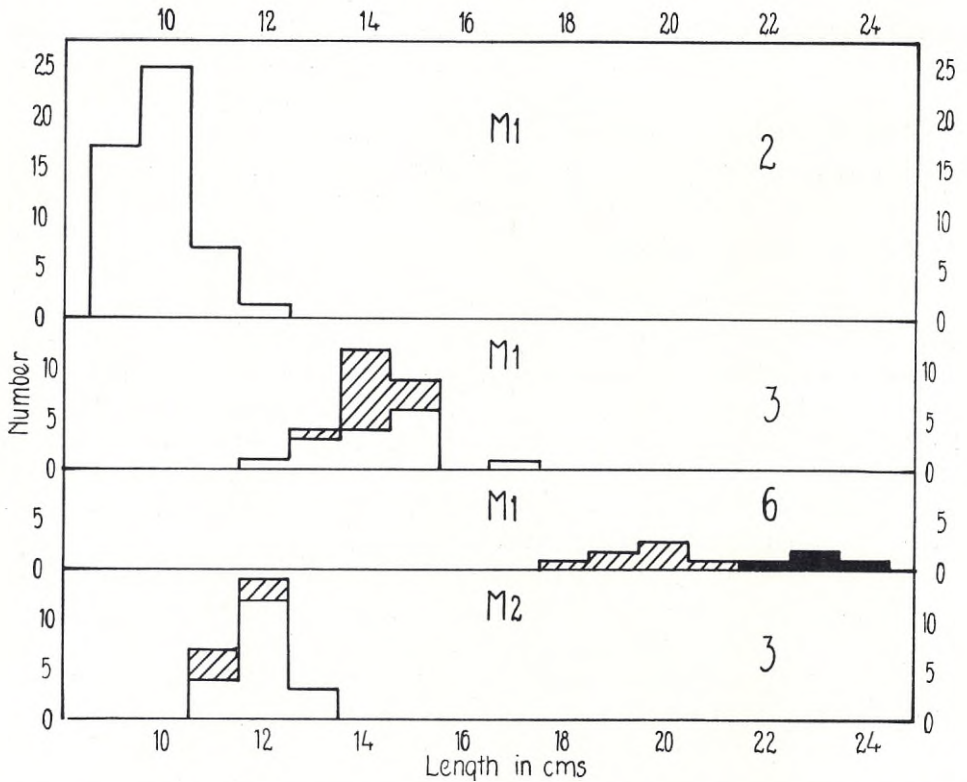


Fig. 52. Roach. Number of mature males and females and of immature specimens in different size groups at different ages in exp. M1 and M2.

the remaining 7 specimens being mature males. The average length of the females now exceeded that of the males by 3.4 cms. The specimens, that had been immature in the preceding year must have been the females, that were mature at the age of 6 years. The above mentioned differences in average length both in this experiment and in experiment M2 therefore show that the growth of the males is slower of that of the females already in the course of the second or third year.

10. Maturity in connection with artificial stocking

What has been said above about the connection of maturity with size and age shall be supplemented by some data derived from certain experiments with artificial stocking at the Kälärne Research Station. With a view of examining the possibilities of using small lakes, free of fish, as fishing waters different species of fish have been released in some of these small lakes in the region of Kälärne. A more detailed account of this activity is postponed

Table 21. *Roach*. Length and maturity at different ages.

Exp.	Age	Number	Percentage			Mean length in cms.				Year of exam.
			Mature		Im-mat.	Total	Mature		Im-mat.	
			♂	♀			♂	♀		
M1	1	150	—	—	100	5.9	—	—	5.9	1946
	2	73	—	—	100	9.6	—	—	9.6	1947
	3	27	44	—	66	14.3	14.2	—	14.3	1948
	4	12	58	—	42	17.1	16.3	—	17.6	1949
	5	12	58	—	42	18.3	17.1	—	20.0	1950
	6	11	64	36	0	20.8	19.6	23.0	—	1951
M2	1	350	—	—	100	4.2	—	—	4.2	1950
	2	112	—	—	100	8.6	—	—	8.6	1951
	3	24	21	—	79	11.8	11.4	—	11.9	1952

to a future occasion. Here we shall only mention some cases in which the above-mentioned connection can be observed.

Of two populations of stocked small river trout in the lakes Grästjärn and Libergstjärn 40 specimens of the age of four summers were caught in the former. Of these 22 were males and 18 females, all specimens being mature, their average length being 29 and 28 cms., respectively. Fishing in Libergstjärn, carried out when the trout were 5 summers old, gave 3 mature males and 5 mature females, but at the same time 4 immature specimens. Here the length amounted to only 21—26 cms., i.e. about the length of specimens of the same age in the more poorly growing pond experiments. Thus on account of the poorer growth some specimens were still immature, although they were one year older than in Grästjärn.

Hybrids between char and brook trout were released in the lakes Nissetjärn and Svarttjärn. When caught again in Svarttjärn at the age of three summers the catch was found to consist of 29 mature specimens, 17 males and 12 females, 10 specimens being immature. The average length was 21.2, 19.5, and 19.3 cms., respectively. In Nissetjärn the length at the same age was 28—35 cms., only one immature fish being obtained as against 9 mature specimens, 5 males and 4 females.

In the lakes Grästjärn and Rörtjärn char was released. The number of specimens caught at the age of three summers was 24 and 51, respectively. In the former lake the length of the specimens, all of them immature, was 22—27 cms., in the latter 27—34 cms., all specimens being mature here. After another year 43 specimens of 27—31 cms. were caught in Grästjärn, of these 2 being males, 12 females, and 19 still immature specimens. The chars in Rörtjärn, all of them mature, 6 males and 9 females, had now an average length of 33.2 and 32.8 cms., respectively.

A great number of experiments with artificial stocking were made with whitefish. These experiments entered in part into certain studies by SVÄRD-

SON (1951) on the taxonomy of these fishes. Thus fry of whitefish of "aspsik" (*Coregonus peled* [Gmelin]) and "storsik" (*Coreg. pidschian* [Gmelin]) from the lake Uddjaure in Lappland were released in the lakes Vontjärn and Ilvåstjärn. In Vontjärn the growth was remarkably good with an average length of 41.4 cms. at the age of 3 years, and of 46.8 cms. at 4 years, while the average length in Ilvåstjärn amounted to only 18.0 cms. at the age of 4 years (SVÄRDSON 1950). According to this author the average length of "aspsik" and "storsik" from Uddjaure at the age of 4 years was 27.0 and 29.0 cms., respectively. At the age of 1 year, however, the average length of the badly growing whitefish in Ilvåstjärn was 10.8 cms. as against only 9.0 cms. for the two species in Uddjaure. Examinations of the maturity of the released whitefish showed that from among the 75 caught 3-year-olds of the fast-growing population in Vontjärn a great number of the males was mature. At the age of four years all of them were mature in either lake, 19 and 46 specimens, respectively. Here it is of interest that in either case maturity was reached at a lower age than in the populations in Uddjaure. In whitefish from Gimdalen which had been released in Svarttjärn all specimens caught at the age of 3 years (summers), viz. 14 males and 16 females, were mature. Their length was 28—34 cms. against only 15.7 cms. in the pond-experiment.

Fry of hybrids between a small whitefish ("smärling" or "sellack", *Coreg. lavaretus* L.) and the above-mentioned "storsik" were released in three other lakes at Kälarne, viz. Långsmaltjärn, Grästjärn, and Västra Rörtjärn. As two-years-(summers-)old the fish caught in the three lakes measured 13—15 cms. (32 specimens), 14—19 cms. (78 specimens), and 27—30 cms. (16 specimens), respectively. The number of mature specimens was 3, 18, and 12 specimens, respectively, or 9.4, 23.1, and 75.0 % of the total number caught. Thus these hybrids became mature rather early, and the percentage of mature specimens increased with better growth and increasing length. Also in the lake Grästjärn 40 three-year-(summers-)old hybrids were caught, 21 males and 19 females, all of them mature and with a length of 18—21 cms.

Hybrids between a big species of whitefish and a small species (*Coregonus albula* L.) were released in the lakes Grästjärn and Hundtjärn. All fish caught at the age of 2 years (summers) were mature. These were 21 males and 10 females, length 21—24 cms., in Grästjärn, and 12 males and 61 females, length 22—24 cms., in Hundtjärn.

Finally a release of perch in Lake Bodtjärn ought to be remembered. Already at the age of 3 years all fish caught, 28 males and 30 females, were mature. Unfortunately their length was not determined. Their growth must nevertheless have been very good, as the average length of 16 males and 14 females caught one year later was 20.9 and 23.4 cms., respectively, thus greater than in the best-growing pond experiments of the same age.

Where a comparison was possible between these experiments at artificial

stocking the results were the same as in the experiments in ponds, viz. early maturity corresponding to good growth rate, and late maturity to poor growth rate.

IV. Informations in the literature regarding the connection between maturity, size (growth rate), and age

As has been mentioned in the introduction informations about age and size at maturity, thus at the first spawning, are quite often met with in accounts of investigations on the biology of fishes. In these cases the aim has usually been the settling of a minimum size of the fish or of the size of the mesh in the fishing gear. As a rule it was only the question of deciding that maturity is reached at this or that age and size. Several fishery biologists have, however, been led to the question, whether or not there exists a connection with the growth rate, and whether or not conditions vary in different lakes or in different regions. Even when such differences have been established, they have in most cases not been further commented upon, and only a small number of investigators has entered upon these problems in greater detail, and in isolated cases made them the object of special studies or experiments.

It has been deemed serviceable to compile from the existing literature a fairly exhaustive synopsis of the more important results as far as the above-mentioned connection is touched upon, in order then to proceed to a comparison with the results accounted for above. We begin with the trout and other salmonids.

I. Salmonids

One of the first to deal more thoroughly with the question of maturity and growth rate in the trout was KNUT DAHL (1910, 1917). In the course of his expansive studies of the trout in different Norwegian lakes and rivers he proved the growth to be generally better in the populations of big-sized trout in the mountainous districts and in eastern Norway than in the populations of smaller fish in the west country. At the same time he stated maturity to be attained earlier in the males than in the females. In the west country this happened at the age of 3—4 years in the males, and at 4—5 years in the females. In the big-sized populations in the east maturity arrived later or at the age of 5—7 and 6—8 years, respectively. Thus the small-sized forms of trout should become mature at a lower age and a smaller size than the large-sized forms. Dahl reports on the other hand that he has not been able to establish in the large-sized forms any differences of age for maturity in connection with different growth rate.

For the Norwegian trout populations also HUITFELDT-KAAS (1927) has pointed to the remarkably varying growth rate in a great number of populations. He also established early maturity to be commoner in small river trout

and in stunted trout populations in small lakes than in big-sized populations. SVEN SÖMME (1930) who also has examined these conditions in Norway finds it difficult to discover such a connection. He also states that in certain cases the growth rate of the males seems to be somewhat better than that of the females. JACOB SÖMME (1934, 1941) believes the age for maturity to be greater than that reported by Dahl, but does not enter more closely into the connection with the growth rate. He also points out that in several cases the males grow better than the females, and mentions furthermore that occasionally the females reach maturity at a lower age than the males. The same information is given by DANNEVIG (1939). In either case the material seems rather too small. Dannevig who has studied the very small-sized populations in the south country has found that there the trout rarely attained an age exceeding 4—5 years, and that maturity was reached at 3 and, in some cases, at 2 years. About trout populations farther north in Norway SIVERTSEN (1953, p. 32) says that "better conditions of growth for the fish gives older age of ripeness". His material was, however, rather small, and the information supplied hardly supports the statement quoted.

On examining a large and fast-growing trout in Lake Vättern and the above discussed small river trout in a little brook near Kälarne I have myself (ALM 1929, 1938, 1939) shown that maturity is reached usually at the age of 4—7 and 2—4 years, respectively. In the trout from Lake Vättern the specimens which had had a good growth rate undertook their spawning migration earlier than those with poorer growth rate. Since the spawning migration is conditioned by the beginning maturity, this observation must indicate that with a good growth rate the maturity started earlier than in the opposite case. By breeding experiments with these two forms of trout I have furthermore established (1949) that this difference in the age at maturity remained unaltered through three generations, and thus must be genetically determined. In connection with the mentioned big trout from Lake Vättern it can be reported that prior to the regulation of this lake and the River Motala ström there had existed in the river a trout that did not descend into Lake Vättern, but attained maturity in the river at about the same age as the real Vättern trout, although it was then on account of poorer growth rate of considerably smaller size (ALM 1929). For a big trout in Lake Kallsjön in the province of Jämtland RUNNSTRÖM (1952) reports that maturity does not appear before the age of 6 years or later. By rearing this form in ponds mature females were, however, obtained already after 4 years. About mature males no information is supplied. For the trout of Lake Storsjön, also this in Jämtland, GUSTAFSON (1951) has found about 90 % of the population to reach maturity at the age of 7—10 years.

STEINMANN (1941) mentions an interesting change in a trout population. A brook with small trout (Bachforellen) was dammed up at Lake Siltsee in Switzerland, and transformed into a lake. In this connection the fish, after

some years, changed their appearance and growth, and came to resemble the big trout in lakes. At the same time happened "Reifeverzögerung", but as no more detailed information on this point is given, it cannot be decided, whether size or age, or both are meant. On comparing the two trout forms *Salmo trutta lacustris* and *Salmo trutta carpione* in Swiss lakes NÜMANN (1953) has found that the latter, with poorer growth rate, might perhaps reach maturity earlier than the form *lacustris*. But he points out, on the other hand, that on comparison of fast- and slow-growing populations of the big *lacustris* form of trout maturity is found to arrive at about 3 years in the former and at about 4 years in the latter. Nümann also points out that in the large form *lacustris* the females grow better than the males. For the big sea trout in the river Vistula ZERNECKI (1958) has found the youngest mature individuals to be exceptionally well-developed specimens. Thus there existed there a certain connection with the size.

In the Anglo-Saxon literature on fishery frequent statements are found about the age for maturity of the brown trout in lakes and rivers, but the subject is seldom discussed in connection with differences in growth rate, e.g. on the transfer to another environment (FROST 1956). SOUTHERN (1935) reports, however, from Ireland that trout from Loch Atorick with a relatively short life attain maturity on the average one year sooner than the better growing trout from Loch Derg.

A certain connection between maturity and growth rate has been demonstrated also for the Atlantic salmon and sea trout. The majority of the male salmon are known to become mature already before their descent (DAHL 1910, NORDQVIST and ALM 1927, ORTON, JONES, and KING 1938, JONES and KING 1952). In certain cases it has here been observed that this applies especially to the bigger specimens of a certain age. Many students of the natural history of the salmon have shown the age for the descent of the smolt to be connected with the size so that a parr with better growth descends to the sea at an earlier age than a slow-growing parr. In addition to this SVÄRDSON (1955) has shown that a higher or lower temperature can to a certain extent advance or retard the descent. Now it has been proved for salmon as well as for sea trout (ALM 1919, 1924, 1934, CALDERWOLD 1930, NALL 1930, and others) that there exists for populations in a certain river an inverse relation between the number of years spent in river and sea before the first spawning migration such that the younger smolt ascend and mature in a later year, and the older smolt in an earlier year after the descent. Maturity should thus to a certain extent depend on age. At the same time the number of years spent by salmon and trout in the sea is fairly small, and concentrated mainly to 2 or 3 years. Thus the above-mentioned inverse relation can not do away with the fact that for a salmon with high smolt age the total age at the first spawning migration becomes higher than for a salmon with low smolt age. And since, as already mentioned, the greater smolt age in a

population depends on slower growth during the parr stage, the higher age at the ascent implies that maturity arrives later at poor, and earlier at better growth rate. The fact, demonstrated by all students of salmon, that the grilse, which start their spawning migration after only a short spell in the sea consist mainly of males shows that, irrespective of the maturity of the males of the salmon prior to the descent, also in salmon and sea trout maturity appears earlier in the males than in the females.

On dealing with the rearing of salmon in ponds OTTERSTRÖM (1933) mentions that maturity appeared at the age of 5 years, but in males and a number of females already at the age of 4 years. For a small land-locked salmon from Norway, called "blege", DAHL (1927) has found the age for maturity to be 5 years, but in some specimens 4 or even 6 years. Thus the age for maturity of the Atlantic salmon seems to be about the same for the salmon in the sea and for land-locked salmon and for salmon bred in ponds in spite of the poorer growth rate in the later cases.

With regard to the salmonid genus *Oncorhynchus* RICKER (1938, 1950) has found that young of the sockey salmon (*Oncorhynchus nerka*) occasionally do not descend, but stay as a special residual form, and reach maturity in fresh water. The investigations and experiments by RICKER (op. cit.) and FOERSTER (1947) have shown that this residual form grows a little better than the land-locked form kokanee, and also matures a little earlier than this form. These two investigators state furthermore (1953) that in the coho salmon some big males become mature at the age of one year. PRITCHARD (1948) asserts the pink salmon to mature at the same age viz. in the autumn of their second year, irrespective of size.

For North America often very detailed accounts are found about the percentage of mature specimens within different groups of age and size in the forms of trout and char occurring there. It ought to be mentioned here that according to KENNEDY (1954) maturity appears in the lake trout (*Christivomer*) of the Great Slave Lake in the course of the 6th to 10th year, and that the earliest maturing fish tended to be those which were largest for their age. Thus there might exist here a certain connection with size. This is corroborated also by information about the lake trout from other lakes. In Great Bear Lake, where the growth of this species is very slow, maturity appears according to MILLER (1947) not before the 13—17th year, the youngest mature specimens being then about 43 cms. long. In Lake Simcoe in Ontario on the other hand MC CRIMMON (1956) has found an extremely good growth rate with maturity already at the age of 6—8 years. At this age the average length was, however, 59 and 70 cms., respectively. For the age of beginning maturity in the lake trout of Lake Michigan VAN OOSTEN (1943) gives 7 years, and DE ROCHE and LYNDON (1955) for the same species in Maine 6—8 years. For lake trout imported into Switzerland and reared in ponds HEINZ and LORENZ (1955) have shown maturity to have appeared in

some males already at the age of 5 years. The length of some specimens of 4 summers was then already 42—48 cms.

On the basis of own investigations and those of others GRAINGER (1953) has shown the maturity of the Arctic char to appear already at the age of 5—7 years in fast-growing populations, but not before 11—12 years in populations of slow growth, the size being the same, 45 cms., in either case. At a higher age the growth rate was better for the males. For the populations of char in Norway SIVERTSEN (op.cit.) reports on the other hand that maturity appears later in the fast-growing populations. In his studies about the effect upon the fish populations of the regulation of Swedish lakes RUNNSTRÖM (1950) has found the char in Lake Torrön to become mature at an age of 4—5 years and a length of 28—30 and 31—34 cms., respectively. He could also demonstrate that in the years following immediately after the regulation the char had exhibited an increased growth rate, and that the spawning char had a lower average age. Although Runnström does not enter upon the question about the age for maturity, his observations suggest nevertheless that with the better growth rate maturity was attained earlier than before. However, certain Swedish mountain lakes contain a very small-sized form of char that becomes mature at a very small size. Also STEINMANN (1945) mentions the occurrence of pigmy forms of char which, contrary to the larger forms, show an early maturity.

About the brook trout there exists quite a number of reports. In general (ALLEN 1956) it is said to become mature at the age of 2 years for the males and 2—3 years for the females. In this connection Allen points out that the larger specimens reach maturity earlier. TESCH (1958) who had studied conditions in brook trout, released in the Talsperre Cranzahl in Germany could observe there a good growth rate with a length of 23—25 cms. at the age of 2 years, and maturity at this age. Basing himself upon his own studies of the brook trout MARTIN (1949) tells that in small brooks this fish attain maturity at a relatively small size, but sea-run stock at a much greater size. In the former case the growth rate was poorer than in the latter, but no information is supplied about the age at maturity.

In the rainbow trout of Lake Michigan GREELEY (1933) was able to establish four types of different growth rate, depending on the age for their descent from the spawning brook to the lake. Here he found that poorer growth retarded the appearance of maturity.

At last some very interesting studies and experiments with several kinds of salmonids shall be mentioned here. It has thus been possible by selective breeding in hatcheries (HAYFORD and EMBODY 1930, LEWIS 1944, MILLENBACH 1950, DONALDSON and OLSON 1955, VLADYKOV 1956, SEGUIN 1956) to obtain stocks of brook trout and rainbow trout with very enhanced growth rate. These stocks have an earlier maturity, both forms maturing now at the age of 2 and sometimes already of 1 year as against 2—4 years as is the

rule in the wild condition. Donaldson makes a special point of the fact that the largest and strongest fish showed the earliest maturity. Vladykov makes certain comparisons also with wild stocks, and asserts that with better feeding conditions (in hatchery or in a lake) maturity is brought about at an earlier age.

2. Coregonids

For the coregonids information about age and length at maturity is rather common, but comparisons of the varying growth rate in different lakes are rare. From what is known about this question from Europe as well as from America it seems, however, evident that in the small species, in which after a few years, growth becomes slow or almost ceases, maturity appears at an early age, whereas the large species, in which growth continues throughout life, reach maturity at a higher age.

For the Swedish coregonids OLOFSSON (1932) was thus able to demonstrate differences in maturity between a slow-growing whitefish from Lake Skepps-träsket and two fast-growing large forms from Lake Stora Lule vatten, both in the northern part of Sweden, with maturity at about 5 and 6—7 years, respectively. OLOFSSON (1934) further mentions that in connection with the transfer of a very slow-growing form from Lake Lomsjön to other lakes its growth rate became much better. Maturity came, nevertheless, at about the same age in either case, viz. mostly at the age of 2 years for males and 3 years for females. RUNNSTRÖM (1944) found that the little slow-growing whitefish, called "smärling", in the province of Jämtland in northern Sweden became mature at 3 years and a length of 14—15 cms., while the big-growing forms of whitefish were mature at 9—10 years. On the transfer of "smärling" to other lakes its growth rate increased greatly. In this connection no information about the age for maturity is given.

The above-mentioned differences in the age for maturity are stressed particularly by SVÄRDSON (1951, 1953) in connection with his detailed studies into the taxonomy of the species of the whitefish. In establishing the different species he does, however, not supply any closer information about their age at maturity. He points out, however, (1953) that the "storsik" that generally grows rather fast and to big size is represented by a stunted form in the little lake Jutis not far from Uddjaur in northern Sweden. Information about the age of this population at maturity is unfortunately missing. For the coastal whitefish of Uppland DAHR (1947) has found the age for maturity to be 2—3 years for males and 3—4 years for females at a length of about 26, 30, and 37 cms. at the age of 3, 4, and 5 years, respectively. Thus the growth rate was good here, but the age for maturity rather low. Dahr tells furthermore that the growth rate was roughly the same for both sexes, while Svärdson is of the opinion that after some years the growth of the males is poorer than that of the females. With regard to the small

species of whitefish, *Coregonus albula*, which usually spawns at the age of 2 years SVÄRDSON (1956), basing himself upon material from Lake Mälaren, has mentioned the possibility that there maturity has been attained later in the year classes which on account of a great amount of individuals have shown a poor growth rate.

In his many papers about the coregonids in Finland JÄRVI has not given any information regarding changes in maturity in connexion with different growth rates. Only for the small whitefish *Coregonus albula* he says (1919) that it in general spawns in its second year, independent of the growth rate. Concerning the Norwegian forms of whitefish HUITFELDT-KAAS (l.c.) subscribes to the opinion that the small-sized forms reach maturity at the age of 3—4 and the large-sized ones at that of 6—7 years. Further he (1912) reports that in the lake Haugatjärnet near Trondheim, where whitefish had been released, and had not only shown an excellent growth rate, but also propagated, maturity was reached already at the age of 5 years.

Growth and maturity of the numerous species of whitefish occurring in Lake Bodensee and in other lakes of the Alpine regions have been dealt with by HAAKH (1929), LECHLER (1934), WAGLER (1937), ELSTER (1944), EINSELE (1943, 1950), STEINMANN (1951), and others. Haakh maintains quite in general that earlier maturity is connected with better growth rate. He mentions furthermore that about 34 % of the "Blaufelchen" become mature at the age of 3 years and the length of about 29 cms., while among "Sandfelchen", which at the same age reaches a length of about 34 cms., and becomes considerably bigger than the "Blaufelchen", only about 18 % had reached maturity at 3 years. We are thus faced here with the above-mentioned higher age for maturity in the larger form or species. Elster has thoroughly dealt with the connection of maturity and growth rate in different populations of "Blaufelchen", and there has found the percentage of mature specimens to increase with growing size within one and the same age group. For this reason maturity is reached earlier in a population of "Blaufelchen" with a better growth rate than in a more slow-growing population. It is of interest that PROBST (1939) on rearing this species of whitefish in ponds in which the growth rate became exceptionally good already in the course of the first year obtained mature specimens at this age. For another species of whitefish called "Reinanken", Lechler stresses the great importance of size for maturity and says (p. 320): "Die Ernährung kann in den ersten Lebensjahren so schlecht sein, dass im Winter, in dem der Fisch dem Alter nach eigentlich laichen müsste, die notwendige Grösse noch nicht erreicht ist, der Fisch muss noch ein Jahr warten". Steinmann at last, in summarizing his own investigations and those of others, says (1951) that the small-sized forms of whitefish in the lakes of the Alpine regions become nature at the age of 2—3 years, but the large-sized ones only later. He has also reared in ponds fry of a small slow-growing and of a big fast-growing species of whitefish,

and has found that also there maturity is attained at a lower and a higher age, respectively, thus as it happens for these species in the lakes.

Conditions similar to those that have been established for the Alpine lakes seem to exist in North America (VAN OOSTEN 1938, VAN OOSTEN and HILE 1947, KENNEDY 1953, and others). The smaller species are reported also here to reach maturity at an earlier age than the bigger ones. According to Van Oosten the mature specimens in one and the same species at the same age are bigger than the immature ones. He also tells that the females have a longer spell of life and grow better than the males. A very interesting case is mentioned by MILLER (1956). By very intensive fishing in a small lake in Canada the age at catch was lowered from 5.1 to 2.3 years. Simultaneously the growth rate rose, and the age at maturity fell from five to two years. Miller pronounces also more in general (1957) that, as a group, fishes are very plastic, and that heavily exploited populations respond by earlier maturity and increased growth rate, but that such changes are not genetic.

3. Perch, pike-perch, pike

Growth rate, age, and maturity of the perch have been studied in a great number of lakes, but only a few investigators have carried out comparative studies of these conditions. In a synopsis from Germany RÖPER (1936) shows that the males, when they have a good growth rate, become mature at the age of 1 and 2 years, commonly, however, at 3 years and at a length of 9—10 cms., the females one year later at a length of 11—12 cms. He sums up by saying (p. 629) that "bei guten Ernährungsmöglichkeiten die Geschlechtsreife früher eintritt". I have found a similar connection between maturity and growth rate for the Swedish lakes and in earlier experiments in ponds (1946, 1952, 1954). Exceptions from this rule were supplied by some very stunted populations, where maturity seemed to arrive at a relatively low age (cf., however, p. 120). Also TESCH (1955) is of the opinion that in populations with a very poor rate of growth maturity is reached at a relatively early age. Basing himself upon a large material from German lakes he thinks, however, that otherwise maturity is reached earlier with a good growth rate, than with a poor one. LE CREN (1958) has during more than 29 years studied a very great material from Windermere lake in England, and has examined especially the growth rate of the different year classes in connection with decrease of the population and the temperature conditions of the different years. He establishes a correlation of faster juvenile growth with earlier maturity. In a general account of growth and maturity in some freshwater fishes LASKAR (1943, 1948) represents another opinion namely that maturity is attained earlier in slow-growing, and at a higher age in fast-growing populations. He points, however, to the existence of many exceptions from this rule. Investigations from America (SCHNEEBERGER 1935,

ESCHMEIJER 1937, HILE and JOBES 1941, JOBES 1952), suggest that a better growth rate brings about earlier maturity. The majority of those that have studied the perch point out that the males become mature earlier than the females, and that their growth rate is poorer. I have also shown (ALM 1952) that the difference in the time for the maturity of the sexes is greater in stunted than in fast-growing populations. Röper and Tesch (loc. cit.) suppose the total lease of life to be shorter for the males than for the females.

Among the remaining *acanthopterygians* there exist for the pike-perch certain informations about the time for maturity and the growth rate. From Sweden studies of the pike-perch in the lakes Toften, Hjälmaren, and Ymsen by ALM (1917), FREIDENFELDT (1922), and VALLIN (1929) show the growth rate to be poorest in Toften and best in Ymsen, while the pike-perch from Hjälmaren occupies an intermediate position. Unfortunately no data on maturity are available from Ymsen. In Hjälmaren the males of the pike-perch reach maturity at the age of 3—4 years, the females at 4—5 years. In the more slow-growing pike-perch in Toften maturity seems, however, to arrive 1—2 years later.

Several species of pike-perch (walley) occur in America. DEASON (1933) who has studied them especially in Lake Erie has found that among the three species found in this lake, viz. yellow pike-perch, blue pike-perch, and saugers, the growth rate is best in the first, and poorest in the last. The length at maturity is greatest in the yellow pike-perch, and smallest in the sauger. It can, however, not be settled, how this agrees with the age at maturity. In examining the pike-perch in the Red Lakes DEASON and VAN OOSTEN (1957) have found maturity to start at the age of 3 years for males, and of 4 years for females, and that at the age of 6 years 100 % of the males and 80 % of the females were mature. RAWSON (1956), however, has found that the walleyes from Lac la Ronge mostly get mature at an age of 8—10 years. No comparable information regarding the connexion with the size are given. Rawson has further on pointed out that from about 7 years age the females grow better than the males. It is of interest that in examinations of the pike-perch (valley) in Lake of the woods and Saginaw Bay CARLANDER (1943) found great differences in the growth and HILE (1954) that maturity was attained earlier in year classes with good, and later in those with poor growth rate.

In the closely related family of the sunfishes HUBBS and COOPER (1935) have carried out comparative studies of growth rate and maturity on two species (*Xenotis megalotis paltastes* and *Apomotis cyanellus*) in the lakes of Michigan. The growth rate was found to be better in the southerly situated lakes, and poorer farther north. Maturity has, however, been attained in both instances mainly at the age of two years in either sex. Thus these species have become mature at a definite age rather than at a definite size. Bigger specimens of a certain age have nevertheless been found to reach maturity earlier than specimens of poorer growth. The males, furthermore,

grew somewhat better than the females, but did not reach the same age. It is also of interest that according to these authors the greatest longevity was attained in the region of the greatest dwarfing, i.e. in the northerly situated lakes. Investigating the rock bass (*Ambloplites rupestris* (Raf)) HILE (1941) found an early maturity connected with better growth rate.

For the pike (*Esox lucius*) the age for maturity is usually given as 2—3 years for males, and 3 years for females. SCHOLZ (1932) has found strongly developed gonads in big-sized pikes of one summer's age in ponds. Also NAWRATIL (1954) and HEGERMANN (1958) have established maturity in fast-growing populations already at an age of 1 and 2 years, respectively, corresponding to the lengths of 32—35 and 41—47 cms. Talking about the pike we can also mention the investigations by UNDERHILL (1949) who has compared growth rate and maturity of the American pickerel in three neighbouring places, viz. a brook, a pond, and a lake, each with its own stock of pike. The growth rate was poorest in the brook, and best in the lake. Maturity was attained in the males at 1—2, 2—3, and 2 years, respectively, in the females somewhat later. As far as the rather scanty material permits the drawing of conclusions, maturity was thus attained at a lower age by the stocks with the poorest growth, and vice versa.

4. Cyprinids

Statements about the growth rate and the maturity in several cyprinids are given by several authors. One of the earliest is OTTERSTRÖM (1930) who accounts for such investigations in the bream (*Abramis brama*), the roach (*Leuciscus rutilus*), the ide (*L. idus*), and the rudd (*L. erythrophthalmus*) in some Danish lakes. He makes, however, no definite statement about the connection of growth rate and maturity. The existing tables and the general statements suggest, however, that early maturity is connected with good growth rate, in some cases, however, also with a very bad one, while the highest age for maturity seems to occur in stocks with a medium growth rate. Otterström points out that the males reach maturity earlier than the females, and that the difference between the sexes in growth rate and size is greater in stocks with poor growth rate.

In examining bream in Swedish lakes (1917, 1919) I have found a rather varying age for maturity, most often, however, 6—8 years, but have not been able to establish any direct connection with the growth. According to JÄRNEFELT (1921) in the very slow-growing bream in Lake Tusuulajärvi the males should become mature already at the age of 3—4 years, the females at 5 years. For the Finlandish populations of bream and ide C. SEGERSTRÅLE (1933) reports that in the inner portions of the archipelagos, where the growth rate is better, maturity is reached some or several years earlier than among the more slow-growing stocks in the outer archipelagos.

WUNDSCH (1940) has stressed the difficulties met with in attempts at

deciding the connection between growth and maturity in wild stocks of certain cyprinids. Basing himself upon examinations of the bream in lakes of Brandenburg he believes nevertheless that maturity is retarded to 6—7 years for instance in a fast-growing stock in Müggelsee as against 5—6 years in stocks with slower growth rate. In a paper by GEYER and MANN (1939) which also is mentioned by Laskar, it is shown on the other hand that the males of very fast-growing populations of bream in the Hungarian lake Fertö and in the Gracian Volvilake reach maturity at the age of 2, and often already of 1 year. In the course of his investigations into the food of the bream LASKAR (1948) has studied also the connection between maturity and growth, and his above quoted statement about the perch applies also to the bream.

In Germany SCHILDE (1936) has found very great differences in the growth of the roach of different lakes, but gives no information about the maturity. This remark applies also to the studies by STANGENBERG (1938) and BALON (1955) of the growth of the roach in Poland and Czecho-Slovakia. This is, however, touched upon in an account, compiled by GEYER (1939, on an extensive material of bream, roach, rudd, and white bream (*Abramis blicca*) from German lakes, Often, however, the number of the specimens from the different localities is small, especially for the intermediate age groups, with the result that his conclusions must be uncertain. Geyer is, however, of the opinion that maturity is attained later at good growth than at a poor one. This might be correct for certain stocks with very poor growth, but the available material does hardly justify this general conclusion in the case of stocks with good or medium growth rate. Geyer also shares Otterstöm's view about the differences in the continued growth of the sexes in slow- and fast-growing stocks. Thus at very good growth the two sexes become mature almost simultaneously, and in the continuation grow roughly at the same rate. WESTFAHLEN (1956) expresses similar ideas about the connection between growth and maturity in the roach.

The very extensive literature about the carp and the breeding of this species in Europe contains very few informations about the age for maturity in connection with better or poorer growth. Usually we find only as a general rule that the males of the carp reach maturity at the age of about 2—4 years, while the females become mature at 3—5 years (WALTER 1934, WUNDER 1936, 1939, 1940, and others). Wunder points out, however, that slow-growing carp become mature later than fast-growing, and that he has observed males that at particularly good growth had become mature at the age of 1 year. BUSCHKIEL (1932, 1937) points to the many factors which here play their part, and says that abundant and suitable food brings about good growth, and accelerates maturity. He mentions especially (1937 p. 465) that in Indonesia the carp has "ein in Europa unbekanntes schnelles Wachstum, in Verbindung damit sehr frühe Geschlechtsreife", i.e. at the age of 1 year.

Buschkiel mentions furthermore that in richly fed and thus overfed carp the gonads are not developed in the normal way with the result that such specimens do not reach maturity. Also LETITCHEVSKY (1954) has shown good growth to be accompanied by earlier maturity. He thus reports that in central Russia the carp reaches maturity at the age of 4—5 years, but in southern Russia, where the growth rate is higher, already at 3 years. In the Caspian Sea maturity appears earlier in the northern than in the southern parts, depending, according to Letitchevsky, on the more abundant food and the higher growth rate in the first-mentioned regions. Also in experiments in ponds he has found an earlier maturity at better growth.

Exhaustive purely experimental experiences concerning such a connection have been made by SCHÄPERCLAUS (1953) with the crucian carp (*Carassius carassius*). On this occasion this author has been able to establish the existence of ecologically and geographically separated races with different, genetically conditioned growth. But it also resulted that growth is likewise dependent on the food supply and the density of the population. While the males reach maturity in general at the age of 2 years and the females at that of 3, Schäperclaus has found that in ponds with very fast-growing populations maturity is reached by either sex at the age of one year and at a length of 6—8 cms. From the beginning of the second year the males grow more slowly than the females which on this account become bigger than the former.

LIEDER (1957), who had carried out experiments with the rearing of hybrids between common carp and crucian carp, found maturity to appear at the age of 2 years at good growth, at a higher age at poor growth. He has also shown the gonads and the ability of reproduction to be less developed in the slow-growing than in the fast-growing hybrids.

For the tench (*Tinca tinca*) H. NORDQVIST (1927) reports that the specimens that had reached a considerable size during the second summer spawned at the age of two years. HERRMANN (1940), who had carried out exhaustive studies into the growth and the maturity of this kind of fish, has on the other hand found no distinct connection of this kind. He furthermore points out that both at poor and good growth the difference in size between the sexes is extremely small.

5. Marine fish

There can here be no question of entering in any detail into the literature on the growth and maturity of marine fishes. It ought to be sufficient to quote GUNTER (1950). Referring to HUBBS and basing himself upon a review of growth and age in several species of fish in the northern and southern seas along the east coast of America he says (p. 299) that "delayed sexual maturity, longer life, slower growth and greater final size are characteristics of animals in colder seas". This would imply that during the first years of

life the growth in the short-lived populations can be the same or better than in the older populations of the same species. As an example the cod can be mentioned. In the Baltic it exhibits a rather good growth in the course of the first years (K. A. ANDERSSON 1954), but does not grow as old and big as the cod in the northern Atlantic. The Baltic cod attains maturity at the age of 3—4 years, the north Atlantic and Arctic cod not until 6—10, sometimes 14 years. Thus early maturity coincides here with a good growth rate during the first years.

The flatfishes mostly display a slower growth in the Baltic than in the North Sea, and attain maturity at a smaller size. Informations about the age at maturity are uncertain. This age is possibly higher in the small-growing populations. According to MOLANDER, who has discussed the results of the fishing experiments with plaice and flounder in the Baltic (1954, 1955), it appears as if with rising growth rate maturity appeared at a lower age, but at a greater length. This would then imply that the age for maturity was higher, when the growth rate had been poor.

In the case of the herring conditions remind of those mentioned for the big and small forms of trout and the species of whitefish. According to K. A. ANDERSSON (op. cit.) the herring races in the Atlantic and the North Sea attain maturity mostly at the age of 3 and 4 years and at a length of 22—25 and 25—26 cms., respectively. The Baltic herring again become mature at the age of 2 years and at a length of 16—20 cms., small specimens at 3 years.

Even when the same species is concerned a bad growth rate can be linked with an early maturation. ELKIN (1955) gives such an example for the whiting. At the coast of Ireland this fish reaches on the average a length of 20—24, 30.5—35.0, and 36—42 cms. at the age of 2, 3, and 4 years, respectively. Most of them reach maturity at the age of 2 years. In the seas off Iceland (SAEMUNDSON 1925) the whiting grows faster, and measures about 40 cms. at 3 years and 45—50 cms. at 4 years. Part of the fish get mature at the age of 3, but most at 4 years.

6. Aquarium fish

To this general synopsis of the connection between growth and age at maturity of fishes in nature might be joined the interesting studies carried out by SVÄRDSON (1943) on the aquarium fish *Lebistes*. As far as I have been able to find Svärdson is the only person who has made this problem the object of special experiments. In these experiments, which dealt mainly with males, he has found these to mature the earlier the better they grow, and that therefore the specimens with the poorest growth have the highest age at maturation. In *Lebistes* the growth of the males ceases with maturity. The males with the best growth that had become mature at the lowest age were therefore smaller than the males which had had a medium growth,

but a somewhat higher age at maturation. The males with the poorest growth again were smaller at maturation, and were thus almost of the same size as the best-growing, while their age at maturation was considerably higher.

On recapitulation this review contains the following.

For trout, char, and whitefish a great number of investigators assert the occurrence of different forms or even species with different growth rate and different size, and with different age at maturity. The small-sized forms are said to become mature rather early, and have a rather short length of life, while the large-sized forms reach maturity at a higher age, and grow rather old. A similar condition is by some investigators stated to exist also in different populations of the same form or species of some cyprinids, sometimes also in perch, and also in marine fish of both warmer and colder seas.

Many investigators assert on the other hand the existence of an exactly opposite condition so that slow-growing populations have a late maturity, while fast-growing ones become mature at an earlier age. This has been asserted for several forms of salmonids, and also for perch, pike, pike-perch, and some species of cyprinids.

Finally many authors mention that the larger specimens of the same age get mature before the smaller specimens, and that generally the males become mature one or two years earlier than the females.

V. Factors inducing maturity and ripeness

For the further elucidation of the connection between maturity, size and age, and before a discussion of the results from the Kälärne-experiments, it appears suitable to touch upon the factors that cause maturity and ripeness and to give a short review of the investigations regarding these questions. In this connection it is of importance to keep these two conceptions apart, since at maturity partly other factors must come into play than at ripeness with subsequent spawning.

Maturity presupposes both a certain size of body and a certain internal development of the gonads. Here we have to remember that in fishes the gonads often begin their development already at an early age. Thus in the *Cottus*, which becomes mature, and spawns at the age of 2 years, HANN (1927) found the oogonial division to begin in the females at the age of about 14 months, and the division of the sperm cells in the males in the autumn of the second summer. In the females a certain development of the gonads takes place almost a year before normal maturity. For *Fundulus* that spawns in the summer MATTHEWS (1938, 1939) has found a gradual increase in size of the gonads almost a year before maturity, and for the minnow, *Phoxinus laevis*, BULLOUGH (1939—40) has demonstrated that maturity starts in the

previous summer, and that in late September and early October the gonads increase very much in size, especially in the females. ZAITZEV (1955), who has studied the cycle of ripeness in the pike, has shown that the gonads undergo a vigorous development already during the late summer that precedes next year's spawning. For the perch these problems have received special attention on the part of TURNER (1919), LE GREN (1951), and KRIZENECKA-PULANKOVA (1952). The last-mentioned author has shown that in the males the weight of the testicles increases already during the first year almost at the same rate as that of the body, while in the females the development of the gonads begins first at a certain length, but takes place then at a much higher rate. Turner and Le Cren have studied the development of the gonads in different months, and have found the testicles to enlarge considerably already in August, when the temperature of the water is at its maximum, while the expulsion of the sperm coincides with the rise of temperature after the winter. For fast-growing one year old male specimens of carp WUNDER (1940) has found that the gonads can develop very quickly, and can reach a weight which is 15—20 times the weight of the gonads of "Hungerformen" of the same age. We also know from hatcheries that in salmonids the development of the gonads starts early in the summer preceding the spawning. The same applies likewise to the development of the gonads prior to the first spawning, thus the maturity. In his experiments with *Lebistes* SVÄRDSON has proved the existence of a positive correlation between weight of body and growth of the male gonads, but he has also found that at a slower increase of body size this correlation is changed so that the development of the gonads appears to be faster. These observations are contradicted by LASKAR's statements (1943) that in a fast-growing population of bream the gonads are extremely small during a number of years in order to increase speedily in size first at a length of the body of about 39 cms., corresponding to an age of 5 years. Such conditions ought, however, to be exceptional.

In warm-blooded vertebrates, including man, maturity arrives at an age and a size which are fairly closely determined for every species. Better or poorer supply of food or certain other reasons can nevertheless cause an advance or a delay of maturity as compared with normal conditions. Such cases are referred to e.g. in HANSSON and BONNIER (1950) from their experiments with the breeding of twins in cattle. In the cold-blooded vertebrates size and age for maturity are subject to much greater changes. Among the scientists, who have expressed opinions on these questions especially with regard to fishes we ought to mention HUBBS (1926), HUITFELDT-KAAS (1927), CRAIG-BENNET (1930—31), BULLOUGH (1939—40), SVÄRDSON (1943, 1951), and LASKAR (1943, 1948). Hubbs especially stresses the importance of the growth rate, and sums up in the following way (p. 75): "The central interpretation advanced in this paper is that either individual or racial modifica-

tions of the developmental rate affect the differentiation aspect of development in the same direction as the growth aspect. Conditions which accelerate the developmental rate accelerate and accentuate the differentiating tendencies as well as the growth tendencies. Retarding conditions operate in the opposite manner. This relation of growth and differentiation is evident in the course of normal development". This consequently agrees with the rule from Kälärne. Hubbs is, however, also of the opinion that fast growth and fast development in the very first years can bring about an earlier cessation of growth, and says in this respect (p. 75): "Accelerating conditions hasten the growth in the early stages, but later bring about a slackening of the growth rate, probably because of their accentuated action on growth inhibitions. Retarding conditions cause a protraction of the early growth, but a less abrupt slackening of the growth rate with age, so that eventually the size attained is often greater than under accelerating conditions".

In reporting on his above mentioned extensive investigations into age HUITFELDT-KAAS (op. cit., p. 245) sums up the question about maturity in the following way: "From these many single observations pointing in the same direction I draw the conclusion that starvation (lack of food) tends to hasten the propagation of the fish and increases its intensity. From a teleological point of view such a theory should be apparently well-grounded. When a fish or other organism is starving to death, it ought to, by all means in its power, as for instance by hastened development of semen, eggs or larvae, work for the upholding of its species — and that even at the price of its own longevity. In the great dispensation of nature it plays, as is well known, a less important part whether the individual organism dies, if only the breed's continued existence is secured". With regard to the forms of trout and in part also the coregonids the results arrived at are without doubt correct, but there we have to do with different forms or races, as mentioned above. With regard to other fish we may be faced with one of the later (cf. p. 119) indicated misinterpretations of the age for maturity. Huitfeldt-Kaas has not undertaken any real experiments.

CRAIG-BENNET on the other hand has carried out a great number of experiments, viz. with the stickleback (*Gasterosteus aculeatus*) which normally becomes mature at the end of the first year and with a length of about 4.5 cms. He says (op. cit., p. 274): "that the initial maturation of the young fish is due directly to a certain size," while ripeness and spawning depend more on external factors and internal secretion from the gonads. As mentioned above BULLOUGH's experiments deal mainly with the normal reproductive cycle of the minnow, and show factors of both temperature and light to play a rôle here. He does, however, not touch on the importance of size.

The above-mentioned experiments by SVÄRDSON with the aquarium fish *Lebistes* were, however, directed amongst others towards the connection

between maturity and growth rate. He was also the first to demonstrate the interesting connection between early and late maturity in fast- and slow-growing specimens of *Lebistes*. Already then and still more so later on (1951) Svårdson has, however, partly on the basis of Laskar's statements, but also of those by myself and others, accepted also the opposite conception. In doing so Svårdson arrives at an explanation of the development of early maturity in stunted populations in lakes, where the food conditions have been unfavourable for a long time, which reminds of Huitfeldt-Kaas' theory. He is of the opinion that in such lakes an earlier maturity could be explained with respect to the continued existence of the species. This continued existence should be assured by natural selection favouring specimens with a genetically determined earlier maturity. For this Svårdson finds support in his experiments with *Lebistes* since he had shown there, as mentioned above, that with poor growth of the body the size of the testicles exhibits a relative increase, and that with a poor supply of food spermogenesis itself appears in younger and smaller testicles (1951, p. 120). Populations of the type referred to as "sexually mature juvenile forms" would then originate "when the food supply is extremely poor, perhaps also as a result of extremely low temperatures."

LASKAR who is the foremost representative of the opinion linking a bad growth rate with early maturity has based his attitude to a large extent upon HUITFELDT-KAAS' statements and also upon the above-mentioned investigations by GEYER, WUNDSCH, etc. together with other reports found in the literature. His own occupations with the question took place in connection with investigations concerning the food of the bream. Laskar insists mainly upon the importance of size for maturity, although in a direction which is opposite to that found in *Lebistes* by Svårdson. For an explanation he looks to the contradictions existing between the factors, external as well as internal, which influence growth rate and maturity. At a good growth rate the growth factors, according to Laskar, prevail over the factors which produce maturity, while at a poor growth rate the latter gain over the former, and produce an early maturity. Laskar mentions, however, several exceptions from his rule, and points out that for the comparison of populations from different geographical regions his rule is not applicable. It seems also, as if occasionally he took only the size into consideration without at the same time taking into account the age, and he points to the necessity of controllable experiments. It is, however, peculiar that Laskar has paid no attention to Svårdson's experiments with *Lebistes*. In this case he might have modified his point of view.

In this connection also certain experiments with brook trout by SEGUN (1956) have to be mentioned. This author reared fry of brook trout at high temperatures, 50—60°F., and there obtained maturity and spawning already 13—14 months after fertilization of the eggs instead of at an age of 24—25

months in colder water. The length was about 28 cms., thus indicating a very good growth rate during the first year. This early maturity Seguin interprets as a result of the direct action of the temperature upon the inner organs. It appears, however, more probable that it was the growth rate which in this case has been directly influenced by the environment. If so, it was, as in the experiments with carp of BUSCHKIEL, WUNDER, and LETITCHEVSKY, the speedily reached size that brought about the early maturity.

In this connection it is also of interest to keep in mind that an excessive growth resulting from fat-forming food can bring about such a degree of overfeeding of the fish that the gonads do not develop normally, and the fish become sterile. This has been shown for carp by WUNDER and BUSCHKIEL, for trout by ROSSELAND (1937), and for the small whitefish *Coregonus albula* by E. MOLIN (1945).

Even if, superficially seen, age and size, thus the growth rate are the main factors producing earlier or later maturity, it is mainly the secretion of the pituitary gland which, when the gonads have reached a certain size, induces maturity and the first ripening and spawning of the individual. For this reason it can be appropriate to pay attention also to certain experiments dealing with these processes. These experiments aim admittedly more at the ripeness, but are certainly of importance also for the understanding of the problems of maturity.

Here we have to keep in mind that in their natural surroundings our fishes spawn in general only once a year. Only under exceptional circumstances, e.g. for the carp in the tropics, spawning occurs, according to BUSCHKIEL, two or more times a year. This is usual also in aquarium fishes. In most instances the spawning of a fish is more or less genetically tied to a certain season which changes from species to species. Different reasons can, however, produce a considerable shifting of the spawning time, good examples being the species of whitefish and the rainbow trout.

Ripeness is of course conditioned by maturity. But ripeness and especially the spawning depend in addition on a number of releasing stimuli, particularly the rise or drop of the temperature to a certain value, specific for different species of fish, and on the availability of a suitable substratum for the spawning. This has been dealt with in detail by FABRICIUS (1950).

Now the frequently early development in the fishes of the size of the gonads can explain, why under certain conditions the differentiation processes in the gonads, which are necessary for maturity and ripeness, can start earlier than normal. The experiments which have been carried out in this field have, however, dealt mainly with fishes which had reached maturity already earlier, and had spawned already once. Only the above-mentioned experiments with *Cottus*, *Phoxinus*, brook trout, and *Lebistes* have been carried out with juvenile fishes.

In most of the experiments it was intended to induce fishes to spawn

more at the same time and also earlier than normal, partly in order to escape the necessity of saving the fishes kept for breeding purposes for a longer time, and partly in order to obtain an earlier hatching and a longer period of growth, and in this way to get a material which would resist winter better. Sometimes the question was also to induce spawning for instance in fish that had been prevented from reaching its spawning places, and which thus lacked certain necessary stimuli for the release of the spawning. That no attempts have been made to obtain an earlier maturity has probably its reason in the fact that the trout hatcheries would rather have a retarded maturity, since it is believed that the growth rate becomes lower once the fish has spawned. This view is e.g. expressed by TÄGTSTRÖM (1944). We shall show later that this is not a universal rule. Also roe and milt of quite young fishes have been considered inferior in quality compared with that of older specimens. Thus the experiments were mainly aimed at bringing about a change in the time for spawning. For this reason attempts were made at deciding what induces the secretion by the pituitary gland of the hormones releasing the activity of the sexual glands. The experiments were made mainly with factors of light and temperature.

Several investigators (HOOVER 1937, HOOVER and HUBBARD 1937, ROWAN 1938, HAZZARD and EDDY 1950, and CORSON 1955) have succeeded in inducing the brook trout to spawn several months earlier than normal. This they achieved by modification of the light, giving more than the normal daylight in spring, while later on introducing gradually increasing periods of cover. For brook trout and blue back salmon ALLISON (1951) and BURROWS (1957, 1958) could show that continued exposure to light before their normal spawning time retarded ripeness, while individuals of blue back salmon that had been exposed to shorter periods of illumination spawned at least 19 days earlier than normal. BURROWS says (1948) that light, not temperature, apparently is the prime factor in accelerating or retarding sexual maturity. By illumination HARRINGTON (1950) got *Notropis* to spawn three months before the normal time. ROWAN (1938) points out that this influence of the light "appears to be secondary as far as the gonads are concerned" (p. 396), since removal of the pituitary gland produces atrophy of the gonads. He is also of the opinion that the light acts upon the pituitary gland by way of the sight.

Other investigators have found the influence of temperature to be greater than that of light. Here we can first mention the previously referred statements by HUBBS and GUNTER about the importance of the temperature for maturity and furthermore the temperature experiments by SEGUIN with brook trout. By experiments with *Fundulus* MATHEWS (1938, 1939) and BURGER (1939) proved directly that illumination was without importance. Here the important factor regulating spermatogenesis was temperature, low temperatures exerting a retarding influence upon the maturation of the sperm. In the

above-mentioned experiments with *Gasterosteus* CRAIG-BENNET came to the conclusion that the rise of temperature is of the greatest importance for the ripeness. MEDLEN (1951) and HUBBS, CLARK, and KIRK (1957) arrived at the same conception through experiments with *Gambusia* and *Etheostoma lepidum*, respectively. Medlen does not believe this influence of the temperature to take place by way of the pituitary gland, but thinks that there probably might be some stimulation of the gonad directly by temperature. Several investigators (JOHANSEN and JACOBSEN 1921, ALM 1924, 1934) have shown that in years with high temperature of the water the ascent of the salmon into the spawning rivers takes place at an earlier sea-age. And since the ascent is conditioned by the beginning maturity, the higher temperature would here bring about an earlier maturity. Also here we are considering the first sexual maturity. Unfortunately only sparse informations are supplied about a possibly better growth rate during the warmer years or in salmon with an early sea-age. It is, however, probable that this has been the case (ROSÉN 1918), and has influenced maturity in the same way as has been mentioned above for the big trout from Lake Vättern (ALM 1929). In this connection also the above-mentioned statement by SVÄRDSON about the importance of temperature for the descent of the young salmon is of interest. The importance of the temperature for maturity is stressed also by LASKAR. He is thus of the opinion that under certain conditions high temperature can by itself bring about earlier maturity. Of interest are also the observations by SEGERSTRÅLE (1932) according to whom the spawning of bream and other cyprinids can fail to appear, if the temperature of spring and early summer is unusually low. It is thus also conceivable that low temperature, independent of poorer growth, can retard maturity. At last we ought to mention the investigations of DAUBERT and PETERS (1956) who for the aquarium fishes *Chichlasoma* and *Haplocromis* suggest a certain connection between spawning and purely atmospherical factors.

Several experiments performed by the injection of pituitary hormones as well as by extirpation of the pituitary gland prove that the influence of the environmental factors in question does not affect the gonads directly, but by way of the pituitary gland. Experiments of this kind with a greater number of species of fish like carp, eel, pike, minnows, salmonids, sturgeon, river lamprey, and tropical fishes have been carried out since many years in Russia, the Netherlands, and America by, amongst others, LEPKOVA (1956), VAN ORDT and BRETSCHNEIDER (1941), IHERING (1935), HASLER, MEYER and FIELD (1939), BALL, LANSING, and BACON (1954), and ROBERTSON (1955). By such a procedure spawning has often been induced after only a few days, while it should otherwise have taken months or still longer, before spawning took place. A circumstantial review of the literature on this subject has been compiled by GRACE PICKFORD and JAMES ATZ (1957). Although the experiments mentioned now have had the main aim of influencing the time for the

ripeness and the spawning, they have in certain cases been carried out with juvenile fishes, and have in this way also had connection with the time for maturity. This last remark applies especially to the experiments by VAN ORDT and BRETSCHNEIDER in which injection of pituitary extract from the carp produced maturity and spermatogenesis in juvenile male eels. Better growth rate and earlier maturity have been obtained also by the injection with other extracts and hormones, like thyroxin, oestron, and testosterone (SVÄRDSON 1943, and others).

VI. Conclusions from the Kälärne experiments about the connection between maturity, size (growth rate), and age

1. Maturity and size (growth rate) in specimens of the same age and in the same experiments

As could be seen in the previous chapters several investigators have, in connection with the examination of the age in larger catches of fish from natural populations, pointed out that it was mainly the larger specimens within a certain age group that had become mature. In a purely experimental way this has been shown to apply also to *Lebistes*. The experiments at Kälärne show that this circumstance can be considered the rule, since a more or less distinct connection of this kind has been found to exist for all species that have been examined, and for nearly every individual experiment. This appears especially from the Figs. 4—7, 21, 22, 32, 34, 39 and 40. This does of course not imply that all mature specimens are larger than the immature ones. Such a sharp limit does not exist, as can be clearly seen from the Figs. In perch and roach, where after some years the females grow faster than the males, the mentioned connection becomes evident only during the second or third year. Only some isolated experiments with big trout (Figs. 20) and rainbow trout (Fig. 38) have shown maturity to appear more irregularly in both bigger and smaller length groups of identical age.

The connection between size and maturity appears clearly also in the differences in average length of mature and immature specimens of the same age (Figs. 2, 19, 31, 33, 42, and Tables 2, 6, 11, 12, 15, 16, and 17). In the experiments in which the males exhibited a better growth rate than the females, viz. in small river trout and some other forms of trout, in brook trout and hybrids between char and brook trout, in grayling and whitefish, the average length for mature specimens, both male and female, has almost always been larger within every age group than that of the immature specimens. In experiments with species in which the growth rate of the males drops faster than that of the females, especially in the perch, the average length of the immature specimens after some years became larger than that of the mature

males, but smaller than that of the mature females. Thus mature females were commoner among the larger specimens.

This distinct connection between size and maturity at a certain age within a certain experiment implies that the specimens which for one reason or the other have a better growth rate reach maturity at a lower age than the specimens with a poorer growth rate. These latter specimens attain maturity only after one or more additional years. This is especially evident from Figs. 11, 12, 14, 16, 26, 29, 35, 36, and 48—50 in which the different maturity groups have been kept apart. These diagrams also give a certain idea of the size at maturity at different ages within a certain experiment. Thus it is evident that the later mature specimens were on the average smaller than the specimens that after an earlier maturity were now of the same age. Further on in all experiments the average length of the males mostly increased with rising age for maturity. This was often the case also with the females. Only in some experiments with small river trout (Figs. 12 and 16) the average length of the females that became mature one year later was smaller than that of the females matured in the previous year. Thus in this case the females that grew worst, and consequently reached maturity at the highest age were the smallest specimens. It is also conceivable that in such a case, where for some reason the growth rate drops considerably after some years, also the average length of the only then maturing males can turn out smaller than that of the specimens that had become mature at a lower age. This results in a type of maturation which is represented diagrammatically in Fig. 53. *The specimens that through good (A) or bad (E) growth, respectively, reach maturity at the lowest or at the highest age are at the age of maturity smaller than the specimens that become mature at a medium age and with a medium growth rate (B—D).* A line connecting the plots for maturity at different ages will then form an arc of a circle, and agree with the results obtained by SVÄRDSON (1943) in his experiments with *Lebistes*.

The environmental conditions in the different experiments have obviously been the same for all specimens of a certain age. For this reason the results derived from such a great number of experiments prove *that for every age group the growth rate and the reaching of a certain size have been decisive for maturity.* The specimens which on reaching this age were still small have had a poorer chance of becoming mature than the bigger-sized specimens of the same age. As the time for maturity can only be calculated in whole years, the former had to wait one or several additional years before reaching a size sufficient for maturity. At the same time, however, they are then often bigger than were the specimens of the same year class, when they became mature in a preceding year. And in certain cases the specimens that have matured at the highest age are again smaller than those that had reached maturity at an intermediate age. This connection between maturity and size or growth rate can without doubt be accepted as a universal rule

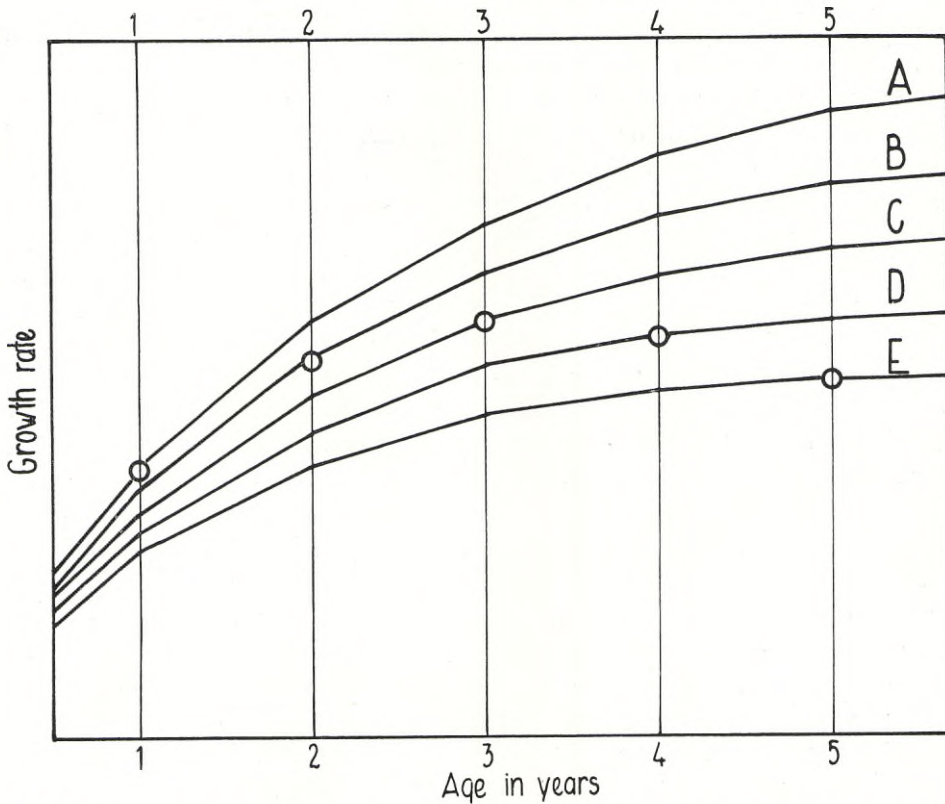


Fig. 53. Diagrammatic growth curves for differently growing individuals within a certain experiment. \circ = maturity.

also for natural populations. It explains the well-known fact that in such populations the age for maturity extends over many years, and also that the size at maturity exhibits remarkable differences.

2. Maturity and size (growth rate) in specimens of the same age, but in different experiments

The now established connection between maturity and size within a certain age class of one and the same experiment ought to exist *a priori* also, if different experiments or different populations of the same species or form are compared with one another. The experiments at Kålarne also show such a direct connection to exist. Here it has to be remembered that *within a certain experiment* — or in natural conditions within a certain year class — the age for maturity of specimens with different growth rate refers to a definite year for every specimen. Conditions are different, when we make a comparison *between different experiments*, where we have to do with all

specimens of a certain age with maturity distributed over several age groups. Here it appears natural to choose for comparison the age at which the majority of males or females are mature, irrespective of whether they have reached maturity in this or in a preceding year.

Already the previously mentioned split experiments with small river trout (Fig. 8), big trout from Lake Vättern (Fig. 23), Swiss trout (page 48), hybrids between char and brook trout (Fig. 32), brook trout (page 51), grayling (page 58), and perch (Figs. 43 and 45) have shown, how fast a changed growth rate affects maturity. On the picking out of groups of smaller and bigger specimens that were all of the same age the percentage of mature specimens had in a later year been higher throughout among the groups with larger size. And after transfer into ponds with different densities of population of groups composed of specimens of the same size and of the same age smaller density and the better growth rate resulting from it has led to a higher percentage of mature specimens than at greater density and poorer growth rate.

In the majority of experiments the differences in growth rate, expressed by the average length of all specimens of the same age in each experiment, were much higher than in these split experiments, the differences in the percentages of mature specimens being still greater. In order still better to illustrate this fact we have entered into Figs. 54—56 growth curves for one experiment with particularly good and one with very poor growth rate, each for small river trout, big trout from Lake Vättern, and perch. Figures express the percentages of mature males and females for every age. Thus in experiment F4 97 % of all specimens of small river trout of 5 years were mature, against only 53 % in experiment F3C. At the same age 54 % of big trout were mature in experiment V3C as against only 29 % in experiment V3A. And in perch of 2 years 98 %, thus almost all specimens, were mature in experiment Ga against only 13 % in experiment F. This remark applies also to the immediately preceding and following year groups. In these examples the good growth and the speedily attained larger size have, in three of these experiments, resulted in almost 100 per cent maturity in perch and the small river trout, and a maturity of 50 % in the big trout, while in the three experiments with poor growth rate and small size only one half of or even fewer specimens have reached this stage. The diagrams at the same time show very clearly the above stressed difference in age of maturity in these forms and species.

The experiments have, however, shown the existence of certain exceptions. For instance, in experiment F2B with small river trout the percentage of mature males was unusually high at the age of three years, and also experiment F3A at the age of 5 and 6 years showed a rather high percentage of mature males. In the latter case the sex ratio was clearly shifted towards the males. For the big trout from Lake Vättern the exceptions occur mainly in

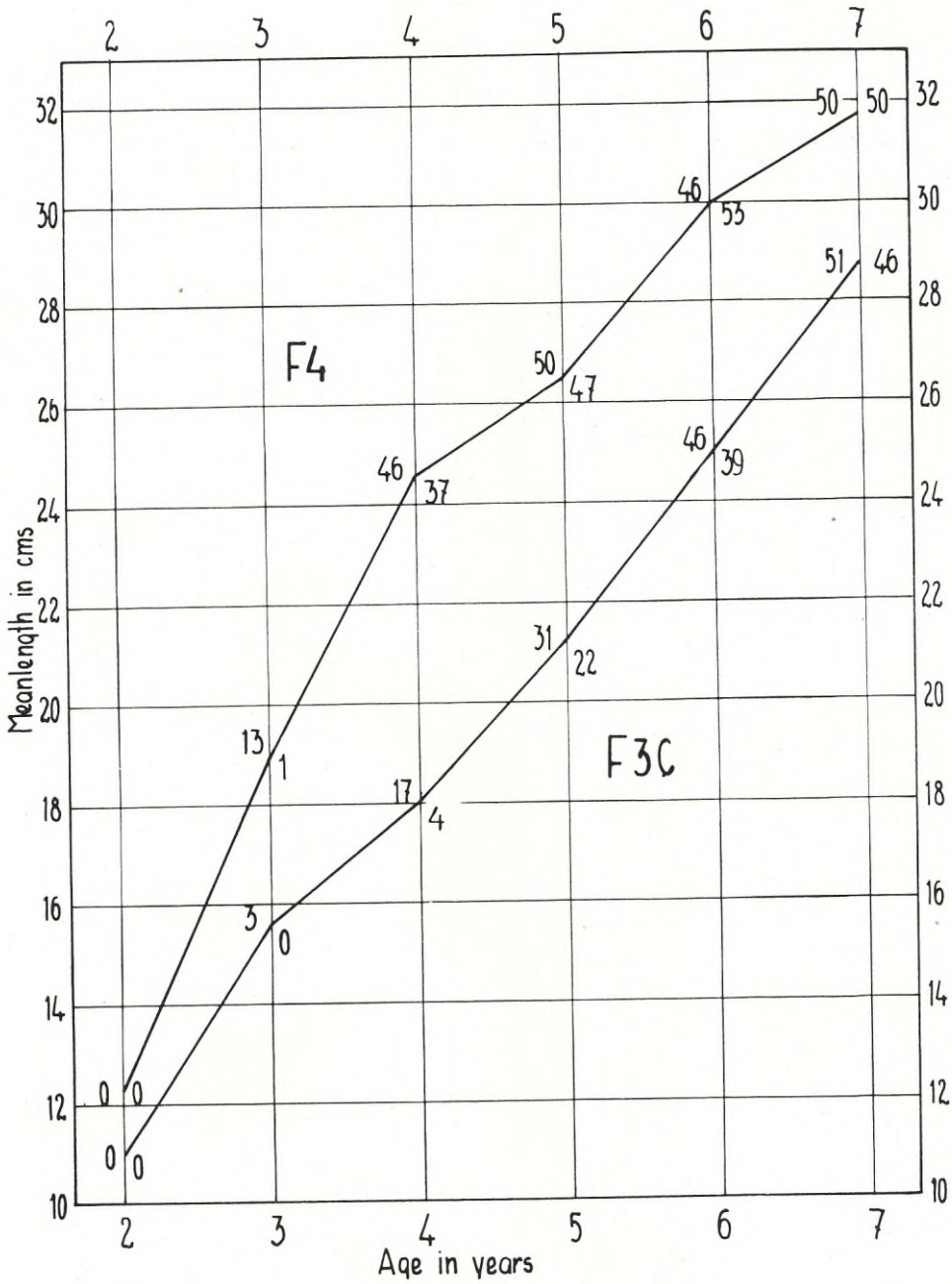


Fig. 54. Growth curves for a fast and a poor growing experiment with small river trout. The figures at the curves indicate the percentage of mature males (to the left) and of mature females (to the right).

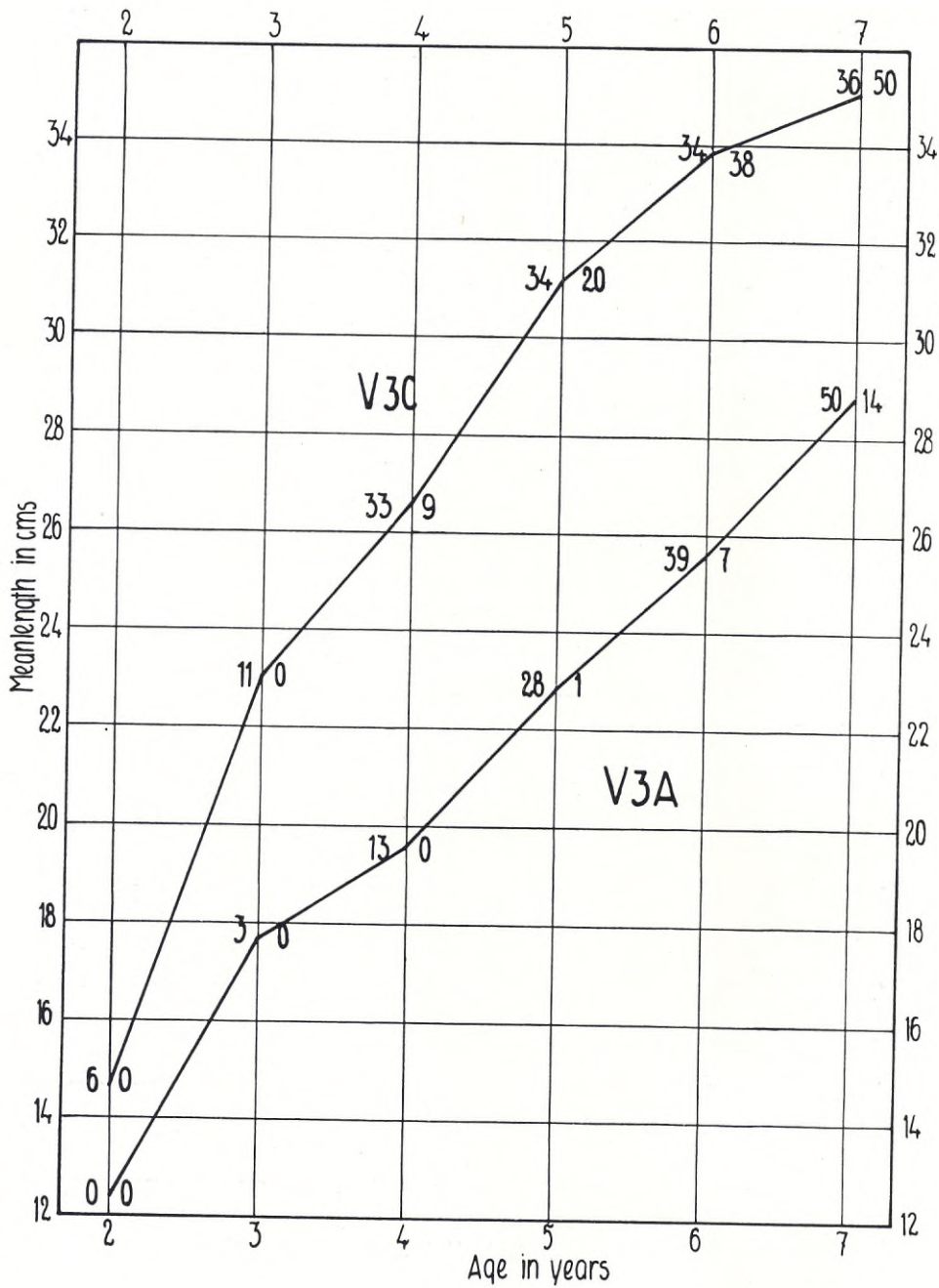


Fig. 55. The same as Fig. 54, big trout from Lake Vättern.

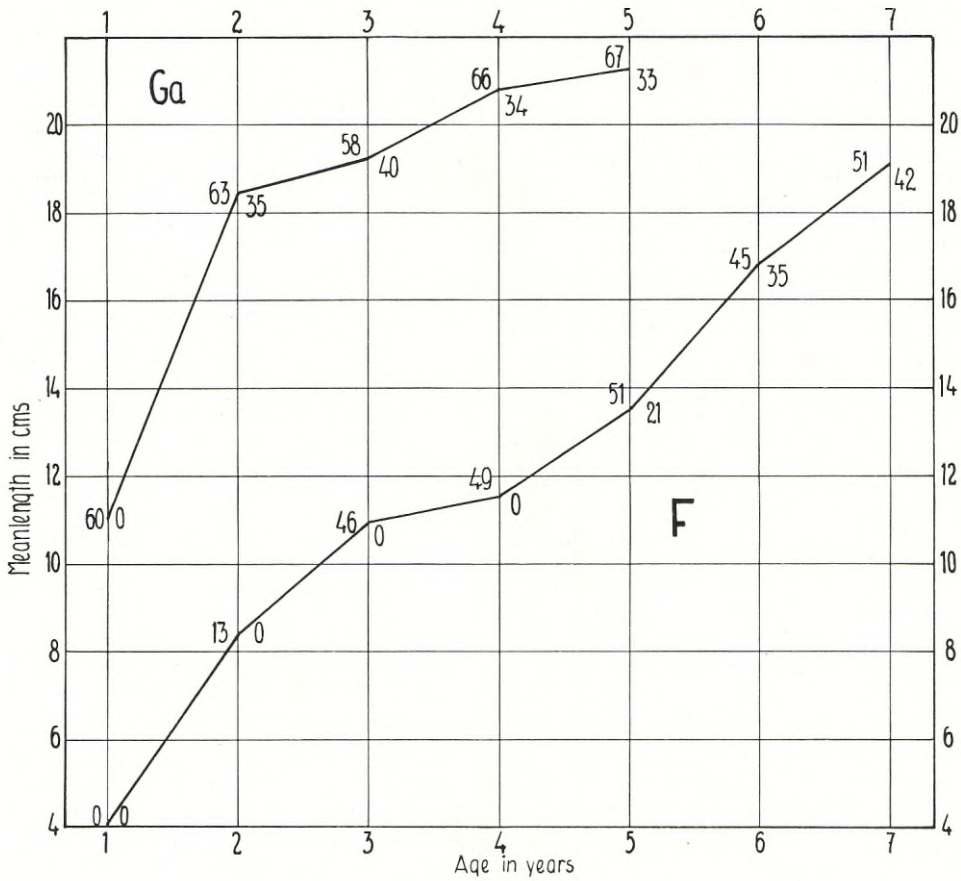


Fig. 56. The same as Fig. 54, perch.

experiments V3B and V3C. Also here we have probably to do with a shifting in the sex ratio, in experiment V3B in favour of the males, in V3C of the females (cfr. p. 41).

These deviations can thus be explained in part by a variation of the sex ratio in different experiments. For the numerous and in part very great deviations in the perch another reason must, however, exist. In order to examine this point more closely a splitting has been carried out in Table 22 so that experiments with the same year classes have been collected. We then find that for each experimental series of this kind, which in this case are taken also from the same original material, the connection between maturity and average length in the experiments is very clear. The occurring deviations are quite insignificant. Another feature becomes, however, immediately obvious, viz. that in experiments from different year classes the percentage of mature specimens of the same age exhibits great differences. Thus for 2-year-old specimens all experiments from the year class 1941 show, in spite

Table 22. *Perch* Average length and percentage of mature males and females in some experiments.

♂, 2 years old			♀, 3 years old			♀, 4 years old		
Exp.	Average	%	Exp.	Average	%	Exp.	Average	%
K 37	9.2	52	K 35 c	12.2	21	K 35 x	15.3	26
K 41 c	9.3	43	K 35 a	13.6	27	K 35 c	16.6	38
K 41 a	10.2	41	K 35 b	15.0	24	K 35 a+b+d	19.1	57
K 41 b	11.0	47	K 35 d	17.7	63			
K 41 d	12.5	50						
H 49	7.6	0	K 41 a	12.8	0	F 49	11.5	0
E 49	8.2	12	K 41 c	13.3	0	D 1, 49	14.1	12
F 49	8.2	13	K 41 b	13.9	4	C 49	15.7	15
D 49	8.4	11	D 1, 49	10.3	0	E 49	15.9	19
C 49	9.7	4	F 49	10.9	0	D 2, 49	16.8	55
B 49	11.4	43	E 49	11.6	0	B 49	17.0	39
A 49	11.7	38	D 2, 49	12.1	0			
Gb 52	13.2	54	C 49	12.6	0			
Ga 52	18.5	63 ¹	A 49	14.1	0			
K 56 a	9.7	7	B 49	15.3	2			
K 56 b	12.0	28	Gb 52	14.9	2			
K 56 c	13.2	47	Ga 52	19.3	40			

¹ Also 35 % ♀.

of partly small size, a high percentage of mature males. In the experiments K49 and 56 the percentage of mature males was much lower throughout, and this in spite of the fact that the average length was in part the same. From among 3- and 4-year-old specimens in the experiments from the year class 1949 none or only a small number of females were mature. Also the experiments of 1941 and experiment Gb 1952 showed a low percentage of mature females. For the corresponding sizes and age groups in the experiments of 1935 on the other hand the percentage of mature females was much higher.

The great discrepancies in Fig. 47 can thus be explained by differences in the age for maturity in material of different origin. In experiments from certain year classes this age has obviously been lower than in others. For the 2-year-old males it must furthermore be pointed out that also the experiments Hj42 and K37 clearly had an early maturity. For the latter experiment this becomes obvious also from the high percentage of mature specimens of either sex at the age of 3 years.

About the reasons of these differences the following remarks can be made. Table 17 shows the experiments in question to be derived from several different lakes. For this reason the origin could hardly have affected the age for maturity, even if, contrary to all expectation, the latter should be genetically conditioned in different populations of perch. Another factor must therefore be looked for. As has been mentioned before, several investigators have shown that temperature can affect the time for ripeness and also the

Table 23. *Perch*. Maturity and temperatures (Cf. the text).

Maturity	Experiments	Years	Average months temperatures in the Kälärne ponds						
			June	July	Aug.	Sept.	March	April	May
Early	K37 ♂, 2 years	1938/39	13.9	17.8	17.3	12.1	0.2	0.6	6.3
	K41 a, c, ♂, 2 years	1942/43	12.1	17.5	16.6	10.0	0.3	2.1	7.8
	Hj42, ♂, 2 years	1943/44	16.0	18.6	13.8	10.6	1.0	0.9	4.1
	K35 c, a, b, ♀, 3 years	1937/38	17.9	20.7	19.1	10.8	0.6	2.2	8.0
	K35 x, ♀, 4 years	1938/39	13.9	17.8	17.3	12.1	0.2	0.6	6.3
	K35 c, ♀, 4 years	1944/45	12.6	19.0	17.6	13.5	1.1	2.9	7.1
	Average		14.6	18.6	16.8	11.5	0.6	1.6	6.6
Late	C-H49 ♂, 2 years	1950/51	12.7	15.5	17.7	11.8	0.3	1.3	6.0
	K56 a, b, ♂, 2 years	1957/58	10.9	16.4	14.9	10.1	0.1	1.1	5.5
	K57 a ♂, 2 years	1958/59	12.5	14.8	14.7	12.2	0.9	2.4	9.0
	K41 a, b, c, ♀, 3 years	1943/44	16.0	18.6	13.8	10.6	1.0	0.9	4.1
	A-F49 ♀, 3 years	1951/52	11.2	14.4	16.4	12.8	0.2	1.8	6.5
	Gb52 ♀, 3 years	1954/55	12.3	16.8	15.4	10.9	0.4	1.4	5.4
	C, D1, E, F49 ♀, 4 years	1952/53	11.8	15.8	14.0	9.5	1.2	3.5	8.7
	Average		12.5	16.0	15.3	11.1	0.6	1.8	6.5

maturity. This might possibly apply also to these experiments with perch. An investigation has therefore been undertaken intended to show whether or not the temperature during the later part of the preceding year and in the spring of the year in which a low maturity age was found had been higher than in years with later maturity. Table 17 shows which years might here come into question, and in Table 23 they have been entered together with the compared experiments. The columns on the right-hand side of the Table contain the mean temperatures of the water in the ponds at Kälärne in the months June, July, August, September, March, April, and May. These figures are rather interesting. In the years preceding the years with high percentages of mature specimens, it is an early maturity, the temperatures in the summer months and especially in June and July have been higher, in some cases much higher, than in the corresponding months in years preceding years with late maturity. It has already been mentioned that the gonads in fishes mostly develop very well a long time before ripeness and spawning. Thus it seems that in these perch experiments the higher temperatures in the summer months have induced a low maturity age in the next year. An exception makes the year 1943. The temperatures in June and July were than rather high. In the following year viz. the spring 1944 the age for maturity for 2-year-old males was high (exp. Hj42) but on the contrary low for 3-year-old females in exp. K41 a—c. Perhaps this difference could be explained by the fact that the temperature in August in 1943 was unusually low and the development of the gonads in the females more depending on the temperatures in the later part of the foregoing summer. It is, however, probable that in the now discussed cases higher or lower temperatures during the summer

might be responsible for the differences in the age for maturity in the experiments with perch. The temperatures in the autumn and in the early spring, which have not shown great differences, have probably not been of any importance.

Perhaps also the above-mentioned deviations in certain experiments with trout and also the differences in maturity in natural waters might be explained in the same way. According to the above quoted statements in the literature about the age for maturity in the big forms of trout this age seems to be lower in Lake Bodensee than in the lakes of Jämtland (p. 86—87). In Lake Vättern this age is higher than in Lake Bodensee, but lower than in Jämtland. It can not be excluded that here the more southern or more northern climate has exerted a certain influence, either by the higher mean temperature or by a period of growth that is longer in the former than in the latter case.

The circumstance that such a large number of experiments, carried out with so many species and forms, have given so similar results speaks nevertheless in favour of the assumption that, for one and the same species or form, first the differences in the growth rates produces earlier or later maturity. Also the results obtained with the experiments at artificial stocking point in this direction. The better had been the growth rate and the larger had become the size, the higher has been the percentage of mature specimens, always on comparison of experiments of the same age.

In the same way as *within a certain experiment* mature specimens occur mainly among the better growing individuals, whereas the specimens with poorer growth are immature, and reach maturity only some or several years later, in the same way *comparison between different experiments* shows that *in an experiment with medium or good growth rate a much larger percentage of all specimens reaches maturity at an age at which in a slowly growing experiment the majority of the specimens is still immature*. The differences in the percentage of mature specimens at the same age, but in different experiments can become so great that in one experiment the average age for maturity is 2 or 3 years higher than in another experiment. This can be seen from the Figs. 54—56.

In the experiments with late maturity the average length at which in a certain experiment the majority of the specimens reaches maturity is often higher, but sometimes lower than in experiments with early maturity. Thus also the conditions concerning the size at the average age for maturity agree on the whole with what we have found above for individuals with different growth rate within a certain experiment.

The following results of the experiments can therefore be established: 1) that *the average age for maturity*, irrespective of the growth rate, *shows in different forms and species a genetically determined difference*; 2) that on comparison of differently growing experiments of the same form or species *a bigger or smaller average size at a certain age is accompanied by a higher*

or lower percentage of mature individuals, respectively, and 3) that in experiments with the same form or species, but derived from different years, maturity, probably on account of differences in the temperatures in earlier months can appear at a lower or at a higher age in spite of the circumstance that growth rate and average length have been about the same in the experiments.

What has been mentioned here about the results from the experiments at Kälärne agrees well also with the results obtained from the experiments carried out in hatcheries and ponds, and referred to in the review of the literature. This applies both to the salmonids as in the selection experiments and to pike, carp, crucian carp, and the hybrids between these species.

Applied to fishes in natural conditions and for the same forms and species the above statement must imply the following: In a population with good growth rate maturity appears at a lower age and usually also at a smaller size than in a population with poor growth rate, where maturity is reached only at a higher age and in most cases at a bigger size. In populations with very poor growth rate and high age for maturity the average length at maturity can again be lower, and approach that of the earliest mature and most fast-growing populations.

When here and in the following populations in natural waters with better or poorer growth are mentioned, it is understood that the year classes occurring in such a population show an approximately uniform growth rate. Unless this is the case, e.g. when a certain year class is particularly rich or poor in individuals, and thereby obtains a poorer or better growth, respectively, conditions are of course more complicated.

VII. How is it possible to explain contradictory statements about the connection between maturity, size (growth rate), and age?

Whenever experiments that could really be checked have been carried out, it has been established with regard to the same form or species that early maturity is connected with good growth, and later maturity with poor growth. The question now arises, how we shall explain the statements in literature concerning the opposite connection, viz. good growth rate linked to late maturity, and a poor growth rate to early maturity. To start with it has to be pointed out that in these statements no distinction has often been made either between different species or different forms of the same species, or between different populations of one and the same species or form. In the former case, for instance, the experiments at Kälärne with the two forms of trout have shown that *the age for maturity can be lower in a small-sized form than in a big-sized one, and that this difference can be genetically determined*. Fig. 57 which shows the average age at maturity in all experi-

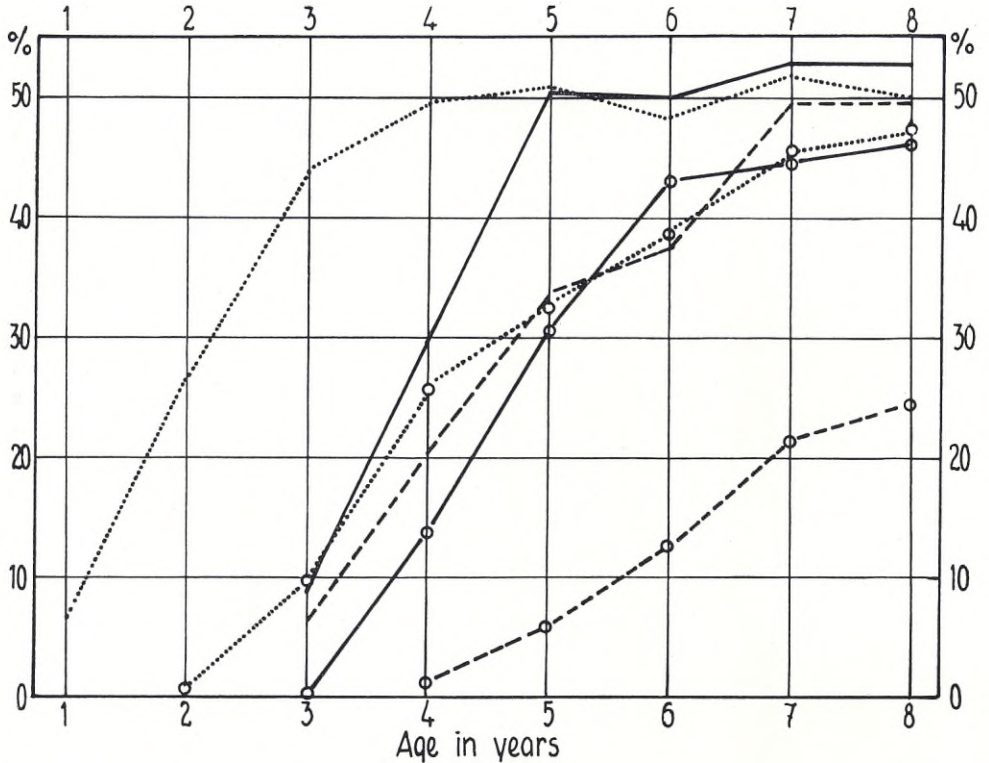


Fig. 57. Connection between age and maturity (in percentage of all specimens) for the total material of small river trout (— = ♂, ○—○ = ♀), big trout from Lake Vättern (----- = ♂, ○-----○ = ♀) and perch (..... = ♂, ○.....○ = ♀).

ments with these two forms of trout indicates that the differences of the age for maturity are very great, especially for the females. But also in the case of the males a considerable difference is seen. Thus 5-year-old specimens of the small river trout contain on the average about 50 % of mature males, such of the big trout only about 34 %. In the diagram has been included also the percentage of maturity for the perch in order to show that the latter is distinguished from the two forms of trout by a still lower average age for maturity.

It is uncertain whether or not the difference in maturity established by these experiments applies also to other big- and small-sized forms of trout. Yet it is conceivable that such genetic characters might have developed in different localities in populations that have been isolated for long times. The investigations by DAHL (1917), HUITFELDT-KAAS (1927), and NÜMANN (1953) into natural populations indicated conditions similar to those that have been observed in the experiments at Kälärne. Here it must be remembered that the mentioned differences in age for maturity apply to forms of

trout which from several points of view can be considered as distinct races. *Within* these races the general rule is valid. In this connection we can refer also to SVÄRDSON'S experiments with *Lebistes* (1943), where stocks with genetically determined difference of age for maturity could be established with certainty.

As appears from earlier statements differences in the age for maturity occur likewise in small and big forms or species of whitefish. For these it is generally reported that the large-sized species reach maturity at a fairly high age and considerable size, while the small-sized ones, which can not properly be called stunted, are said to become mature already at a low age. EINSELE (1952) also speaks about the possibility of the occurrence of "Lokalrassen" within the same species. These should have arisen as the result of long isolation, and have different ages for maturity. The experiments carried out by STEINMANN (1951) which are mentioned above, though without being accounted for in any detail, and which dealt with two forms of whitefish with different growth from Alpine lakes ought to be the only ones which show that the discussed differences might be genetically determined. It appears on the other hand by the experiments at Kälärne that the species "blåsik", a small-sized form with early maturity according to literature, did not reach maturity any earlier than the species "älvsik". And in the above named releasing experiments at Kälärne the age for maturity was low, 4 and 3 years, respectively for species which in their native lakes became big, and thus ought to have reached maturity only at a fairly high age. These examples show that at all events in this species of whitefish no genetically determined low or high age for maturity could have existed.

The above does not by any means exclude that a genetically determined age for maturity, reminding most of the two forms of trout, might exist in other cases. The small-sized species of whitefish, *Coregonus albula*, is without doubt an instance of this kind. This species usually has a short life-span, and spawns already at the age of 2 years. The same applies possibly also to other, as a rule small-sized forms of other whitefish and of char. It is, however, not admissible to compare with them stunted populations of forms or species which normally have a good growth rate. For the herring, in which the small-sized populations in the Baltic become mature at a lower age than the big-sized ones of the North Sea, conditions can best be compared with those for the trout and forms of whitefish, thus with different races. As far as I know there exist no experiments which in this case would show the different ages for maturity to be genetically determined.

Even if genetically determined differences in age for maturity occur without doubt in different forms or species, another explanation of the earlier maturity of small-sized forms and also in populations of the same form or species can be thought of. Thus there is possible that the small-sized species or forms often have a good growth rate during the first few years or at least

during the very first year, a growth rate which in many cases is certainly better than that of the big-sized ones. Thus SVÄRDSON's growth curves for the different species of whitefish (1951, 1953) show that at the beginning the small-sized "blåsik" grow better than the "storsik", this relation occasionally continuing up to the age of 3—4 years. The same applies to a certain extent also to the other small-sized species "älvsik" and occasionally also to "planktonsik". Only in one instance, from the lake Skeppsträsket, the growth rate of the "blåsik" for the first year has been reported as below that of "storsik". And RUNNSTRÖM's (1944) growth curves for the small-sized whitefish, "smärting", show this during the first year to have a greater average length than the large-sized species "storsik". It has also been pointed out above (p. 84) that during the first year the bad-growing whitefish released in Lake Ilvåstjärn at Kälärne reached a greater average length than the stock in Lake Uddjaure from which it was derived. HUITFELDT-KAAS points out also that small-sized species of *Coregonus* can have a rather good growth during the first years, while large sized forms that become old grow slowly throughout their life.

In his above-mentioned studies of the trout in some lakes and rivers in Jämtland RUNNSTRÖM (1952) mentions that on being reared in ponds descendants of these forms of trout became mature at the age of 4 years, while in the natural waters maturity did not occur before 6 years. The size of these later forms during the first year is given by Runnström as from 4.8 to 5.8 cms. No length is given for the trout reared in ponds, but at the age of 4 years the weight was 250 gms. on the average. This ought to correspond to a length of about 30 cms. In the wild trout the length at 4 years was, according to Runnström, 23.3—26.2 cms. As far as can be seen from these figures the growth rate during the first years has thus been better in the trout in the ponds. Also LASKAR (1948) reports that during the first years the large- and small-sized populations of bream display the same growth. "Sie wachsen beide gut" (p. 143). And according to GUNTER (1950) it is a general rule for marine fish in cold seas that they admittedly become bigger there than in warm seas, but that the initial growth is poorer than in the latter case, where maturity comes earlier. As mentioned above also the cod in the Baltic Sea and in northern seas shows the same conditions.

Provided these facts are of general validity they must to a certain extent alter the conception of maturity as well as of size and age in small-sized forms or populations of the same species in so far as the age for maturity is not genetically determined. These forms and populations evidently exhibit a good growth rate during the very first years even if they do not attain any larger size. In this they equal or even surpass many large-sized forms and populations. It does then not seem excluded *that the good growth rate during the first year or the first few years can explain the early maturity in accordance with the fundamental rule admitted on the basis of the experiments*

at *Kälarne*. To this must be remembered that the small forms or species of whitefish mostly after some years are subject to less favourable environmental conditions than the bigger ones. Even if both types occur in the same lakes the former will, by reason of their biologically determined assembling in large schools, be exposed to a strong competition for food. An additional disadvantage in similar cases has been pointed out by MARGARET BROWN (1946) in her interesting studies on the growth of the brown trout. The dense crowding results in a mechanical disturbance which in turn causes increased activity and thus an increased demand for food. These two circumstances bring about a slower growth rate, and the latter also an increased metabolism. With the support of the above-mentioned statements and examinations by HUBBS and SVÄRDSON it seems permissible to suppose that this fast deterioration of the growth rate accelerates the differentiation processes, mainly in the gonads, which in their turn produce maturity. This will then be reached earlier than would otherwise have been the case. In this connection also a statement by LARKIN, TERPENNING and PARKER (1956 p. 84) ought to be remembered, namely that "changes in metabolic efficiency may be primarily a function of size and not of age".

At last we must have in mind that the mentioned statements in the literature are often based only upon the examination of maturity in natural populations, and not upon real experiments. It is then possible that a great part of these information do not express the actual conditions. For this several explanations could be given, without for this reason doubting the reliability of the investigator in question. Thus already SCHÄPERCLAUS (1953) hints at the possibility of misinterpretation of the age as an explanation of the partly contradictory statements. It appears quite probable that this is what has happened in several cases. Also the material might not be sufficiently representative. In general the commercial fisheries make use of gill-nets, fyke-nets, and trap-nets with defined size of mesh. This often results in a certain selection of the catch. Among the younger fish only the largest specimens will be caught, and among the older ones sometimes a higher percentage of the smaller ones will be caught than of the bigger specimens. It is furthermore possible and even probable that the large-sized species often become mature at an age that is lower than that reported, but that this is not observed, since they are not caught before they have reached a certain size and the higher age connected with it. On the other hand it can happen quite easily that among small-sized populations mainly the larger specimens from a certain year class are caught, and these specimens had become mature on account of their better growth rate. It is then easy to believe that this age is the normal one for maturity in the population in question, whereas in reality maturity does perhaps not appear before one or several additional years. This is probably the way in which to explain certain statements that can be found about a low age for maturity in populations of perch and

cyprinids which grow slowly also during their first years, especially from larger lakes with several kind of fish. In such cases it is possible to suppose that the small size is restricted to certain year classes, particularly rich in individuals, of the species in question or of other species which compete with one another for the food. Growth is perhaps better during past or future periods. The experiments with perch at Kälarne show that such small growth, restricted in time, does not lead to early maturity. Experiment F was specially intended to produce slow growth as the result of a very high density of population, and thus to imitate a small-sized population. Provided that the earlier statements were correct, maturity ought then to appear at an earlier age than in the experiments with medium growth rate. In this experiment the growth rate was poorer during the first 4 years (average length at 4 years only 11.5 cms.) than what is usual in small lakes with stunted populations (ALM 1946, 1952). But the experiment showed nevertheless the highest age for maturity. Only a small number of mature males was found at the age of 2 years, and at the age of 4 years still no mature females were found.

Against the above mentioned statements by HUITFELD-KAAS and SVÄRDSON concerning the causes for an early maturity in stunted populations the question could also be raised, why the age for maturity, which surely has first become higher and higher on account of the poorer growth, should suddenly gradually drop as the result of the supposed selection, and at last reach a value that is lower than in the normally growing populations. We should like to see it from a point of view which is the reverse of that occupied by these investigators. If together with increasingly small growth maturity arrives progressively later, then the number of spawning females becomes more and more limited. This ought to have the result that the new growing-up year classes become increasingly poor in individuals. From this ought then to result a better growth rate, something which from the point of view of the species might be as advantageous as a great number of spawning females and an excess of population.

However, on account of the difficulties encountered in attempts of arriving at certain conclusions about the age for maturity under natural conditions *all statements about an early maturity in small-sized and stunted populations have to be accepted with certain reservations*. It is therefore possible that the earlier statements, made both by myself and by other authors, about a maturity which in slow-growing populations of perch and cyprinids was said to be earlier than in fast-growing ones did not always correspond to the actual conditions. Erroneous conclusions like those just mentioned have certainly entered into these statements. The remarks made here can apply also to statements about late maturity in large-sized populations.

The preceding observations concerning deviations from the above proposed general rule, both with regard to the statements in literature and to the experiments at Kälärne, thus show that in a great many cases such divergent statements *can have quite natural explanations*. It is also peculiar that it has not been possible in connection with any real experiments to obtain proofs for the opinion held by LASKAR and others, viz. that in the case of the same form or species a poor growth rate should induce early maturity, while a good growth rate should be responsible for later maturity. All real experiments about the connection between maturity and size or growth rate have on the contrary proved the opposite relation.

VIII. Maturity, size, and age

The discussions in the preceding chapters both of the results obtained in the experiments at Kälärne in comparison with the statements in literature and of the experiments carried out by different investigators on the factors inducing maturity and ripeness give the following picture of the connection between maturity, size (growth rate), and age.

To begin with *the age at maturity* the experiments at Kälärne as well as investigations into fishes in natural surroundings have shown that *this can be genetically determined, and thus on the average lower or higher in different species and also in different forms or subspecies*. To be brief we can say that the age for maturity is relatively high in the majority of cyprinids which probably also become fairly old, but rather low in perch, pike, and also in the most small-sized species as smelt *Osmerus operlanus* L.), stickle-bass (*Gasterosteus*), bleak (*Alburnus lucidus* H.), minnows (*Phoxinus*), and others. These species are, except of perch and pike, in general rather short-lived. In such species a low age at maturity is obviously a necessity for the continued existence of the species.

In the salmonids we find both early and late age for maturity and also a smaller or greater length of life. Much seems to indicate that in the large-sized and relatively long-lived species or forms of trout, char, and some whitefishes the age for maturity is high, while it is lower in those which often are of small size, and which probably not live to the same high age. For the trout at least it has in certain cases been established that these differences in the age for maturity are genetically determined. Both the experiments at Kälärne and the numerous statements in the literature about maturity and growth rate in trout show furthermore that the small-sized forms display a slow growth rate already during the first years. Yet they have nevertheless an earlier maturity than the large-sized forms which mostly grow faster from the beginning. This remark might perhaps be valid also for different forms of char.

With regard to the whitefishes it is advisable to take up a hesitating attitude until reliable statements and results from experiments are available. In spite of the fact that much suggests that also here the large-sized forms sometimes have a higher age for maturity than the small-sized ones several facts can be adduced against the genetic determination of this relation. This has already been referred to above. There exist no experiments that would show that, as in the forms of trout, the initial growth rate of the latter is poorer than that of the former, but nevertheless leads to an earlier maturity. The experiments at Kälarne point on the contrary in the opposite direction. For reasons mentioned above the age for maturity might also be lower in the large-sized, and higher in the small-sized ones than what examinations in natural populations seem to indicate. To this has to be added the circumstance, alluded to on p. 118, that in many cases the small-sized forms or species of whitefish in the course of the very first years exhibit a better growth rate than the large-sized ones but after some years will come into unfavourable environmental conditions, which accelerate the factors inducing maturity.

Thus, in so far as the statements about the differences in the age for maturity in small- and large-sized forms or species of whitefish are correct, it seems as if this difference could depend upon two reasons. *Partly the age for maturity can be genetically determined, thus in the same way as in the different forms of trout.* Then maturity appears at a lower age in the forms or species of small size which also exhibit a poorer growth during the early years than in the large-sized ones. *But the differences can also be of a merely phenotypic nature, and can depend on a better growth rate during the first years in the small-sized forms or species, and on the faster metabolic processes conditioned by it and further accelerated by the later change to bad environmental conditions and a slower growth rate.*

It is possible that also in small-sized and stunted populations of other species or forms similar conditions can lead to an apparently too early maturity.

By the above discussions apart from the age also the factor of size has been introduced. In several of his papers SVÄRDSON has stressed the importance of simultaneously paying attention to both factors, to age as well as to size. In this connection he has proposed the term *physiological age* which would then designate the result of the real calendar age and the size. The application of this term can, however, become difficult in practice. It is admittedly easy to say that two fishes of the same age, but of different size, or two fishes of the same size, but of different age have a different physiological age. But since size can not be defined in similarly distinct units as age, it is very difficult to decide, when two fishes have the same physiological age, and in general to compare the physiological age of different specimens or populations. I have therefore considered it preferable when dealing with

maturity to keep the two factors, age and size, apart. This excludes by no means, according to what has been said above especially about the white-fish, an intimate mutual connection of these factors.

The question about the age for maturity in these forms and species leads, however, from a discussion of the importance of the age for maturity to that of the size. *In the case of differently growing populations of a certain form or species everything seems to indicate that there the size factor is of decisive importance for the appearance of maturity.* It must be admitted that the size, thus indirectly the growth rate, can be genetically determined in different species, and perhaps also in different forms, but there exist nevertheless hardly many groups of animals in which the growth rate is as labile as in the fishes. On this point there exists a complicated cooperation of the factors which influence the growth rate, mainly of abundance and nature of the food, the space, greater or lesser abundance in the occurrence of the same or of other kinds of fish, conditions of light and temperature, acidity of the water, etc. It is often difficult to decide which factor or which factors are the most important.

As a general rule it can, however, be assumed that an abundant supply of food and usually also a high temperature favour the growth rate, while a poor supply of food and a low temperature bring about a slow growth. On the basis of the above discussed experimental results the following can also be considered as definitely established. *A population of one and the same species or form which from the beginning exhibits a good growth rate reaches maturity at an earlier age than a population in which the growth rate is slow already during the first years.* In the former case the good increase in the size of the body brings about also a good growth of the gonads together with an early differentiation both of these and other inner organs, and a general acceleration of the metabolism with early maturity as the result. In the latter case the development of all organs is retarded, and the metabolism is slower. The older the fish, the stronger is, however, the influence of the inner factors which with growing age affect the maturity. It is for this reason that processes of differentiation gradually begin, and that maturity takes place. *In either of these extreme cases the size of the body at maturity can be relatively small, but the age at maturity is low in the former, and high in the latter case.* The average size of the population, however, is larger in the former than in the latter case. *With a medium growth rate and a resulting age for maturity which is intermediate, when compared with the just mentioned border-line cases, the average size at maturity is, however, greater.* A population with such a growth rate of medium quality obtains perhaps a later age for maturity than a population in which the growth rate was high at the beginning, but soon slowed down, and resulted in a smaller average size of the population.

Apart from the size, and independent of it probably *also the temperature can exert a certain influence upon the age for maturity.*

The Fig. 58 contains diagrammatic representation of the now discussed different cases of maturity. The left part of the diagram shows types of growth of species or forms with a genetically determined age for maturity. Two main types can be distinguished here: A) Large-sized, mostly rather long-lived species or forms with an initial good growth and a late maturity, and B) small-sized species or forms with either at first good, but soon slower growth or with slow growth already from the beginning, a lesser or greater longevity, and an early maturity. The right-hand part of the diagram represents different types of growth for populations of the same species or form. Here it is possible to distinguish four types: a) Populations with very good growth rate and maturity at an early age, b) populations with very poor growth rate and maturity at a high age, c) populations with a medium growth rate and maturity at an intermediate age, and d) populations in which the growth rate is particularly good during the first years in order to become poorer later for some reason or the other, and with early maturity. These types of growth and maturity are encountered in large-sized and small-sized as well as in long-lived and short-lived species or forms. A particularly fast-growing population a) of a normally large-growing species or form with late maturity, A (big trout from Lake Vättern) can then in part reach maturity earlier than a very slow-growing population b) of a normally small-sized species or form with early maturity, B, (small river trout). This is seen in Figs. 54 and 55 for the experiments V3C and F3C. It can also be pointed out that the types c) and d) represent the two examples given by GUNTER for growth rate, age, and maturity in cold and warm seas, respectively.

We have not dealt here with the causes which produce the differences in the age for maturity in different species and forms, where this age is genetically determined. We can only point out that in this case a connection must exist with the speciation in itself. Regarding maturity in different populations of the same species or form we have to do with a direct or indirect influence by the environment which expresses itself first of all in different growth rates.

IX. The influence of maturity on the growth rate

As is well known it is a general opinion, and has in many cases been proved as a fact that maturity has a growth-inhibiting effect. This is frequently asserted as a rule which should apply to all animals. Thus HUBBS (1926, p. 59) writes: "The general growth inhibitions as is well known, often are associated with the ripening of gonads, the attainment of maturity being

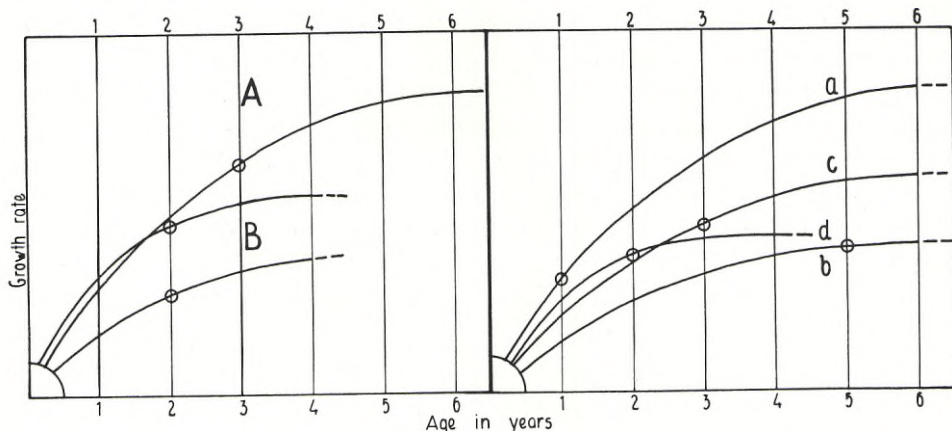


Fig. 58. Diagrammatic growth curves for species or forms with genetically conditioned age of maturity (to the left) and for populations of the same species or form, where the age of maturity is conditioned by size (to the right). o = maturity. Cfr. the text.

marked by a cessation of growth in warm-blooded animals, and usually by a sharp decline in the growth rate in the case of fishes and other animals exhibiting indeterminate growth. Accelerating conditions hasten the inception of maturity and the associated decline in growth rate."

For fishes the same attitude is upheld by BROFELDT (1915), OLSTAD (1919), HUITFELDT-KAAS (1927), OTTERSTRÖM (1930), WALTER (1934, 1940), GEYER (1939), WUNDER (1939), J. SÖMME (1941), TÄGTSTRÖM (1944), STEINMANN (1945), SIVERTSEN (1951), and others. This view is often explained by the statement that growth and development of the gonads make such high demands on the supply of nutrition that only a small part of the food can be utilized for increased growth of the body. The opinion is furthermore held that the general condition of the fish is weakened by the energy spent in spawning. Especially in the case of fishes in which the males grow more slowly than the females there is a tendency of linking this fact with their earlier maturity. Thus, e.g., WALTER (1934, p. 813) writes: "Wir wissen, dass die Geschlechtsreife einen hemmenden Einfluss auf das Wachstum ausübt. Demnach wird es in erster Linie diese um ein Jahr früher eintretende Geschlechtsreife sein, die zum Zurückbleiben der Milchner gegenüber den Rognern führt". STEINMANN (op. cit. p. 414) says quite in general about the small forms, especially among the coregonids, that "Die Frühreife hat ein verzögertes späteres Wachstum im Gefolge, sodass die normale Wachstumskurve deutlich abgesenkt erscheint". Also WUNDER makes use of the same argumentation in the case of the carp. But he points out at the same time that this growth-inhibiting influence of maturity applies only to the males, while in the females conditions are the opposite (op. cit., p. 610): "Das männliche Geschlecht wirkt sich also wachstumshemmend aus und erzeugt

die Hungerform, das weibliche Geschlecht wirkt sich als wachstumsfördernd aus und erzeugt die Mastform". It appears queer that the influence of maturity should be so different in males and females. However, also other opinions have been given. Thus, SCHÄPERCLAUS (1953) basing himself upon his experiments with crucian carp points out that the above-mentioned conception can not be universally valid, and NÜMANN (1953, p. 311) writes: "Auf Grund der Befunde soll vor allen Dingen gegen die Anschauung Stellung genommen werden, dass die Verlangsamung des Längenwachstums direkt auf die Energietransformierung für die Gonadenentwicklung zurückzuführen ist." In the same way LARKIN, TERPENNING and PARKER (1956 p. 90) say that "it is known that many species of fish grow after spawning and continue to grow measurably over the whole of their life span". We have also to remember in this connection that in several species of fishes the males become larger than the females in spite of the fact that they reach maturity at a lower age.

In a great work with the title "Wachstum, Geschlecht und Fortpflanzung" SEITZ (1939) has devoted detailed studies to these questions, dealing, however, mainly with the conditions in mankind. He points out that the growth depends first of all on the endocrine functions of "Schilddrüse, Hypophyse und Thymus", and says about it (op. cit., p. 140): "Man kann daraus schliessen, dass alle drei Einsonderungsdrüsen für die Wachstumsvorgänge im gesunden Organismus etwas beitragen. Sie haben alle einen fördernden Einfluss auf das allgemeine Körperwachstum. Von dieser Regel macht nur eine innersekretorische Drüse eine Ausnahme, das ist die Keimdrüse, bei einem jugendlichen Individuum entfernt, so geht das Wachstum nicht nur in derselben Weise wie bei einem nichtkastrierten Tier weiter, sondern sein Körperwachstum hält länger an, die Verknöcherung der Epiphysen erfolgt später, die Körperlänge wird grösser, die Tiere werden länger als die nichtkastrierten. Es hat also die Keimdrüse auf die Wachstumsvorgänge einen gewissen hemmenden Einfluss. Diese Feststellung ist von grundsätzlicher Bedeutung." According to SEITZ the cause of the inhibiting effect of sexual maturation upon the size of the body is thus not that accepted by the fishery biologists quoted above. But then, Seitz has not dealt in any detail with the cold-blooded animals, and nothing in the literature indicates that experiments aimed directly at the now treated problems have been carried out with fishes in the wild. It should, however, here be remembered that MARG. BROWN (1956) in her experiments with brown trout, has found that in 2-year-old fishes the annual growth rate exhibited "a spring maximum, rapid summer growth and an autumn check, coincided with maturation of the gonads, when they became 3 years old" (op. cit., p. 143). Nothing shows, however, that the growth of these trouts should have been slower in the continuation, we only are told that ripeness itself caused an accidentally passing drop of the growth rate.

With aquarium fishes, however, different results have been obtained. In

the course of his experiments with *Lebistes* SVÄRDSON, who realized that here the main rôle was played by processes of endocrine secretion, carried out several experiments with sexual hormones given with the food. He thereby found that such a hormone from one sex stimulated growth in the opposite sex. This he tries to explain by the assumption that the hormones of the opposite sex should have a destructive influence upon the growth-inhibiting hormones of the own sex. The experiments dealt mainly with males in which growth normally ceases with the maturity. This SVÄRDSON sums up by saying (1943, p. 21): "Die Einwirkung der Geschlechtsreife auf das Wachstum ist also insofern klar, als es die um diese Zeit in den Gonaden produzierten Hormone sind, die das Wachstum hemmen". In another passage of the same paper (p. 45) Svärdson generalizes this statement so as to apply to all fishes.

After this review we shall examine the conditions of fishes in nature, and more especially the results obtained in special experiments. Already the study of the growth curves for a great many species of fishes in natural populations, found in the papers of different investigators, enables one to establish that these exhibit a very often smooth, gradually decreasing curvature, and not by any means the sharp decline at maturity reported by HUBBS. It is obvious that for a population in which the extension of maturity over several years produces a certain levelling effect the curve should show a smoother curvature than for a single individual. Equally obvious is that the growth rate, especially that referring to length, decreases with rising age. Under favourable conditions, however, a vigorous growth can continue through several years in spite of the fact that the individual fishes or the population have reached maturity already early, and that renewed ripeness and spawning have taken place many times over. The above-mentioned experiments with the transfer of small-sized whitefish (OLOFSSON 1934, RUNNSTRÖM 1944) show also that in the new favourable environment growth has increased considerably in spite of the fact that the fishes had been mature already before the transfer. The same applies to experiments with small river trout (ALM 1939) and with perch (ALM 1946). The generally accepted inhibiting influence of maturity upon growth can therefore not be of the same order of size in fishes in their natural conditions as in aquarium fishes or in the warm-blooded animals. Neither am I aware that in the above quoted experiments at selective breeding in salmonids earlier maturity, obtained in connection with better growth, should have been established as having an inhibiting effect upon growth.

Now the experiments at Kälarne have shown with full evidence that the growth-inhibiting effect, which on the basis of investigations in other animals maturity is obviously bound to have, is overshadowed by the innate ability of increased growth which is found in fishes. Experiments with small river trout (Figs. 11—17), big trout (Figs. 26—30), hybrids between char

and brook trout (Figs. 35—37), and perch (Figs. 48—51) supply definite proof for this assertion. On examining the Figs. 54—56 which illustrate the time for maturity in experiments with very varying growth rate one finds that the growth curves, based upon the annually increasing average length of all specimens, show a fairly uniform rise for both good- and bad-growing experiments. Only in experiment Ga with perch the curve describes a strong bend from the 2nd to the 3rd year in order to continue fairly uniformly afterwards. Provided that the maturity of the males should have had a growth-inhibiting effect this ought to have found its expression in a drop of the curve already after the 1st year, when almost all males were mature.

The same thing appears, when the different maturity groups are kept apart. In practically all experiments these groups have in the continuation shown a slowly decreasing growth, but a growth that in the earliest mature groups continued as long as the duration of the experiment. The best example is provided by experiment F3C (Figs. 11—13). Here the losses have been fairly small, spawning has taken place every year in all or in most of the individuals, and the growth rate has nevertheless been good. The sooner maturity had been reached, the greater became the size of these specimens. There exists no deterioration of growth after maturity. The same, though less distinct, appears in the other experiments. It would then be most peculiar, if conditions in nature should be different. What has been reported above about the results of the examinations of age and growth rate in natural populations provides no support for such an assumption.

The results of the experiments at Kälärne show, however, also another interesting condition. As can be seen from the mentioned diagrams and the accompanying account on the experiments, the growth was in the continuation better throughout in the individuals which by reason of good growth had become mature at an earlier age than in the specimens with poorer growth and later maturity. For this reason the different maturity groups still exhibited in many cases a certain difference in size at a time, when all individuals had reached maturity. For the average length this difference could occasionally be fairly great even if on account of the rather large spreading the size curves of the groups partly overlapped each other.

This circumstance can hardly be explained otherwise than by the assumption that the specimens which from the beginning had had a better growth rate grew better also in the continuation. It is difficult to decide, whether this depends mainly upon genetic factors, or upon the greater competitive ability of the individuals which from the beginning had had an advance in growth. It can, however, be pointed out that the experiments with separation of larger and smaller specimens, which in certain cases have been distributed over different ponds with about the same amount of fish by weight, have shown that the experiments comprising the smaller individuals also in

the continuation exhibited a poorer growth than the groups composed of larger specimens. This might perhaps speak in favour of a genetically determined difference in the ability of growth in different individuals.

Examinations of the age in natural populations show likewise that in general certain individuals have had a good growth throughout lifetime, others again a poor one. Several scientists (DAHL 1917, ALM 1924, WILLER 1929, VAN OOSTEN 1938, TÄGTSTRÖM 1944, HOBBS 1953, LIEDER 1956, HASKELL and GRIFFITHS 1956, etc.) especially stress that it is in most cases the size reached during the first year which is decisive for the continued growth. According to DAHL this is valid already from the roe onwards the size of which leads to larger or smaller fry. For the whitefish Van Oosten (op. cit., p. 209) reports that an advantage in size reached in the first year was generally maintained throughout life, and HOBBS (p. 565) says that "the effects of factors which determine size as yearlings have a marked influence on size at subsequent ages". LIEDER says definitely that the different initial growth is often maintained, and that this can have genetical causes, but also depend on exogenic disturbances. HILE (1941) on the other hand could not find such a correlation in the rock bass, and MARG. BROWN (op. cit.) has pointed out that the difference in size which soon appears in an experiment often depends upon a greater competitive ability and a greater power of self-assertion in certain individuals.

Several of the mentioned circumstances suggest, however, that the better or poorer growth rate, as it appears in the experiments at Kälarne, is to some extent genetically determined. This idea is supported also by the above-mentioned experiments at selective breeding of salmonids. There by the systematic selection of more fast-growing individuals, populations with high growth rate, which was obviously inheritable, have been achieved. In his experiments with crucian carp SCHÄPERCLAUS (1953, p. 65) has also demonstrated, "dass es möglich ist durch Auslese der besten Vorwüchser im ersten Lebensjahr einen Zuchtstamm zu gewinnen, der wesentlich bessere Leistungen aufweist als der Durchschnitt der Karauschen". Also at the station at Kälarne certain experiments in this direction have been carried out. Unfortunately lack of space and first of all of tanks and other appliances necessary for such experiments prevented the continuation of the work.

Summing up the results of the experiments we can say that *in fishes under natural conditions the inhibiting influence of maturity on continued growth is not as great as has been shown in other cases. The factors, both inner and outer, which regulate the growing ability are stronger than the growth-inhibiting sexual hormones.* This can be expressed also by saying that the growth does not depend mainly upon maturity, but that it is on the contrary maturity that depends on the growth as has been pointed out already in preceding chapters. For this reason there is no connection between the appearing maturity and the often rapidly decreasing growth rate, e.g. in

small species of whitefish and other small-sized fishes. It depends instead on the circumstance that these species of fish after some or several years with favourable feeding conditions come under the influence of the above-mentioned less advantageous conditions, especially poorer supply of food. This aims both at the amount and nature of the food, and the fish's ability of profiting from it. That there exist also forms or subspecies of the same species with a genetically determined earlier or later maturity has already been pointed out. The same is the case also with the growing ability which may be in itself genetically determined. A bleak (*Alburnus alburnus*), for instance, can never reach the size of the pike even if it comes under the very best conditions with the most abundant food, etc.

It can also be established that in general *the specimens that from the beginning have a better growth rate continue to grow better also later on than the specimens with a slow initial growth, and that this is independent from the time at which maturity is reached.*

X. The influence of maturity on mortality and longevity

In the foregoing has been pointed out that neither the experiments at Kälärne nor studies of natural populations of fish have shown the growth inhibiting influence, which maturity has often been thought to bring about, to be especially striking. In addition to this the experiments provide certain starting points for forming an opinion on the influence of maturity on mortality and longevity.

A certain natural mortality depending on purely physiological processes, on diseases, scarcity of food, and predators gradually appears in all animals. This natural mortality is fairly variable from species to species. Among the fishes perch and the majority of cyprinids reach as a rule a rather high age — 10—15—20 years ought not to be unusual —, whereas many salmonids often do not reach a higher age than at most 8—10 years. Longevity is generally believed to be connected with the metabolic processes. For marine fishes this is directly asserted by HUBBS and GUNTER in the passages quoted in the foregoing. Thus fish living in warmer seas are said to have a shorter life than the same species in colder seas, the faster metabolism being given as reason. Also in the freshwater fishes it is obviously the metabolism that determines mortality and longevity (PEARL and MINER 1935, GERKING 1957).

Now this mortality is often said to be higher in males than in females. Thus many authors mention a tendency towards a decreasing number of males, while the females are said to be relatively common among the older age groups. These assertions are, however, not based on special experiments, but merely an expression of the fact that the percentage of males in the catches of older fish becomes lower. Numerous determinations of the sex in fry and juvenile specimens have shown that at this time the sex ratio is 1 : 1,

or have even occasionally shown a certain preponderance of the males. This applies especially to fishing during the spawning time, and first of all to the perch. In this fish, when caught during the time for spawning, the number of males can reach 80—90 per cent of the total catch, especially in small lakes with stunted populations. Fishing with large-meshed gear in lakes with large-sized populations has, however, often yielded 70—80 % of females (ALM 1952). For walleyes HILE (1954) gives the number of males of about 10 years as only 16—28 %, and for *Coregonus albula* SVÄRDSON (1956) reports the percentage of the females often to exceed seventy per cent already during the 3rd year. For young of the Atlantic salmon a sex ratio of about 1 : 1 has been observed (ALM 1943, HULT 1947, and others), and the same applies according to FOERSTER (1946) to the young of sockeye salmon. At the same time several authors agree in the assertion that generally the catches of larger salmon and trout contain more females than males, as a rule about 60 and 40 %, respectively. LIEDER (1955) has reported on an interesting fact in certain populations of the cyprinid *Carassius auratus gibelio* (Block), where occasionally the females form a great majority already from the beginning. In isolated cases males are altogether missing. The females seem to propagate parthenogenetically, yet according to Lieder not before an inefficient fertilization by males from closely related species has taken place.

It is not surprising that the number of males should decrease in the catches of fishes in which the males grow more slowly than the females, when the fishing is carried out with nets of coarser mesh, and is directly aimed at the catching of larger fish. In this case the scarcity of the males need not derive from their earlier death. In several salmonids and other fishes, however, where in certain cases the males on the contrary exhibit a better growth, some other factor must be responsible for the decrease in the number of males in the older age groups.

Regarding to the opinion of most fishery biologists this should depend on a higher mortality of the males conditioned by their earlier maturity. It is accepted as a general rule that on the average the males reach maturity 1—2 years before the females. This has been distinctly shown by the Kälärne experiments, and is mentioned in practically all investigations into maturity in both fresh- and saltwater fish. Divergent statements are restricted to some exceptional cases. Thus J. SÖMME (1941) and SIVERTSEN (1953) report that they have found trout populations in which the females reached maturity earlier than the males. They omit, however, to give further details. And in his experiments with crucian carp SCHÄPERCLAUS (1953) has found that with exceptionally good growth rate both sexes became mature at the age of 1 year, but that otherwise maturity follows the general rule.

The view that maturity by itself should cause a higher mortality, and thus cause earlier disappearance of the males as the result of their earlier maturity ought to be based upon the reports on these questions that are found in

the general literature. In their experiments with *Daphnia* MAC ARTHUR and BAILLIE have shown already in 1929 that metabolism increases with rising temperature, and that the duration of life varies inversely with the intensity of the metabolism. They found furthermore that in the males the metabolic rate was higher, and the duration of life shorter. The authors discussed these conditions also for other groups of animals, and entered likewise into a discussion of the different chromosomic set-up in the sexes as a possible, though hardly acceptable explanation.

A synopsis of the earlier investigations into this subject has been given by HAMILTON 1948. With the aim of demonstrating the greater mortality of the males he has collected in a table a great amount of figures representing the sex ratio in younger and older specimens of several groups of animals. Among fishes figures are given for both freshwater and saltwater forms but they only show what has been mentioned already above, viz. a preponderance of the females among older, and sometimes almost the opposite among younger specimens. As a general rule HAMILTON (op. cit., p. 313) says "that a lesser viability of males than of females characterizes most of the species of animals investigated so far". "Mortality rates in males are higher than in females and the average life-span is shorter". This HAMILTON believes to depend in part upon the greater number of pathological conditions in the males. But he also considers it possible that the heterozygote sex which is usually the male sex should be more short-lived on account of disturbances in the genes. But in this case the same ought to apply also to such fishes, birds, and insects, in which the sex chromosomes are homogeneous in males. Yet also there the males show the higher mortality.

Also SVÄRDSON has entered upon these questions, and writes (1951, p. 120): "Besides, it seems as if physiological death follows sexual maturity in so far as an individual or a population that attains an early sexual maturity also dies earlier. This is very striking in the different sexes of many fish, the males, as a rule, being sexually mature one or two years earlier than the females and also dying earlier." The first assumption is admittedly correct for certain small species of whitefish, but for reasons that have been given in the foregoing it can not be accepted as an explanation of an earlier death. The later part of the statement is, like the statement by several other fishery biologists, based only upon the more abundant occurrence of females among older fish of a certain year class. Later (1957), however, Svärdson points out that older specimens can cease to grow. In this case it is easy to misjudge their age, neither is it certain in that the assumption of their earlier death will hold good here.

In opposition to the now mentioned statements the results of certain experiments carried out by ROBERTSON (1955) with young of king salmon can be referred to. Comparison between males that had spawned and immature fish of the same size and age revealed no differences in the continued growth

Table 24. Sex ratio at higher ages in the Kälärne-experiments.

Species	Age	Number				%		
		Total	Mature		Im- mat.	Mature		Im- mat.
			♂	♀		♂	♀	
Small river trout	7	615	328	276	11	53	45	2
»	9	342	183	159	—	54	46	—
»	10	250	126	124	—	50	50	—
Big trout	7	533	262	115	156	49	22	29
»	9	283	168	60	55	59	21	20
»	10	235	152	66	17	65	28	7
Small×big trout	6	58	35	23	—	60	40	—
Brook trout	5	108	47	57	4	44	53	3
Char×brook trout	6	143	59	84	—	41	59	—
Grayling	6	87	43	44	—	49	51	—
Whitefish	7	76	39	18	19	51	24	25
Rainbow trout	6	57	41	16	—	71	29	—
Perch	4	1,728	854	446	428	49	26	25
»	7	571	282	278	11	49	49	2
»	9	408	198	204	6	48	50	2

or condition. In spite of the fact that this experiment was carried on only for a rather short time ROBERTSON (p. 39) nevertheless draws the conclusion that "age appears to be the deciding factor in determining death and survival."

The experiments at Kälärne lead to a similar conception both with regard to mortality in general and the explanation of the supposed higher mortality of the males. Mortality in general has often been fairly high in the different experiments, as has already been reported in the accounts of the results. Yet it has hardly been connected with the age for maturity, the longevity having been fairly much the same in experiments both with early and late maturity in either good- or bad-growing specimens. In case any connection with the age for maturity should exist, the length of life ought to have been shorter in experiments or in individuals with early maturity. Several of the Tables show that this has not been the case, rather the reverse. Also earlier investigations (HARKNESS 1922, SCHNEEBERGER 1935, ALM 1952) have shown that for instance the perch attains a higher age in small lakes with stunted populations than in lakes with good growth. This I have assumed to be explainable through the absence of fishing and predators in the small lakes. Apart from this the facts show that the perch can become very old in spite of a rather early maturity and the circumstance that they attain ripeness, and spawn almost every year. Similar results are reported by HUBBS and COOPER (1935) from their above-mentioned experiments with sunfish. Theirfore maturity does not seem by itself to be of such importance for the longevity of a fish as has often been asserted.

The same remark applies to the mortality of males. As has been mentioned in the text the experiments give no evidence of a noticeably greater mortality

in males than in females. This was the case in only one experiment with perch. In order to throw additional light on mortality we have assembled in the attached Table 24 figures from the Kälärne-experiments for the numbers of males, females, and immature specimens at higher ages. (Cfr. also Tables 3, 7, and 18.) This Table shows a sex ratio of roughly 1 : 1. In brook trout and in hybrids between char and brook trout a certain preponderance of the females was seen, while in big trout and rainbow trout the males were in the majority. But otherwise the sex ratio has remained remarkably constant in spite of the fact that the age has risen as high as 9 years for perch and 10 years for trout.

This observation is thus in contrast with those made in the wild. In order to find an explanation we have to return to what has been said by the scientists quoted above about the more intense metabolism of the males as the cause of their earlier mortality. In doing so two points have to be kept apart. On the one hand we have the physiological death, directly conditioned by metabolism itself, on the other hand the different outer behaviour of the sexes which is indirectly determined by metabolic processes, and can bring about a greater mortality in one sex than in the other.

It is thus well known that in all species of fish the males are more active than the females, that they remain for a longer time upon the spawning grounds, and that they expose themselves much more than the females. All this must have the result that the males are exposed to predators and to being caught in fishing gear in a much higher degree than the females. Since on account of the earlier maturity of the males these factors start to act upon them earlier than upon the females, the males must disappear at a faster rate, and among the older individuals of a year class the females must become the majority. To this has to be added that the males which have had the best growth rate, and which therefore have first become mature, and have participated in the spawning, will be caught to a greater extent than the males with poorer growth rate and later maturity in the same year class. This will still further reduce the number of the large-growing males especially in the species of fish in which the males grow worse than the females.

The experiments at Kälärne show that the above-mentioned factors are the most important ones for the explanation of the disappearance of the males. In the ponds at Kälärne no males are removed by fishing, and no predators exist which might reduce the number of males more than that of the females. The consequence is that the males survive, and that at a higher age both sexes are represented by about the same number of individuals. This suggests that the mortality brought about by purely physiological reasons can not be perceptibly higher in males than in females. I have also shown (1952) that in the above mentioned small lakes with stunted populations of perch males and females are about equally numerous in spite of the high age. This must

be attributed also here to the absence of predators and to the circumstance that no fishing takes place in these lakes.

The above must be interpreted as indicating that, compared with other factors of an external nature, also in natural populations the purely physiological mortality is of subordinate importance for the explanation of the disappearance of the males. Also other authors have expressed similar assumptions. Thus DAHR (1947) and HILE (1954) believe for whitefish and walley, respectively, that the disappearance of the males is in connection with their higher exploitation in comparison with that of the females.

In the aquarium fishes the physiological mortality might possible play a greater rôle, since SCHOEMACHER (1944), while making special experiments with *Lebistes*, has found that the sex ratio which at the beginning had been 1 : 1 after one year had been changed to 1 : 4. This change he ascribes to a lesser viability in the males.

XI. Summary

1. At the Kälarne Fishery Research Station a great number of experiments have been carried out with different species and forms of fish, the aim being a study of the connection between first sexual maturity, size (growth rate), age, and longevity.
2. Informations found in the literature about this connection have been referred to, and have been found contradictory in many respects. The reasons of this circumstance have been discussed in detail. Also the factors influencing maturity and ripeness (spawning) have been dealt with, and several earlier experiments on this subject have been mentioned.
3. The results of the experiments at Kälarne in comparison with experiments of earlier dates and the above-mentioned reports in general are believed to justify the following conclusions with regard to the just mentioned connection.

a. Within a certain experiment (a certain year class) and in specimens of the same age maturity is reached earlier by larger than by smaller specimens. Thus in every age group the growth rate and the attaining of a certain size decides the maturity. The specimens which on account of a good growth rate reach maturity at a low age are then of a smaller average size than the specimens which on account of medium growth rate reach maturity at a higher age. The specimens again which grow particularly badly, and which therefore become mature at a still higher age can in certain cases exhibit at this age an average size which is below that of the specimens matured at medium growth rate.

b. The comparison between different experiments (different year classes and populations with year classes of the same growth rate) reveals different cases.

ba. The age for maturity can be genetically determined in different species and also in different forms of the same species. It is then usually higher in large-sized and often fast-growing forms than in small-sized and often slow-growing ones. This is exemplified by big and small forms of trout, and perhaps also by similar forms of char and whitefish.

bb. In different experiments or in different populations of the same species or form the age for maturity depends mainly on size, thus indirectly the growth rate. With an initially good growth rate maturity is reached at an earlier age than with a from the beginning poor growth rate. In the former case the good growth rate has applied also to the inner organs, amongst others the pituitary gland and the gonads. The metabolic processes were relatively fast with consequent differentiation processes in the gonads and early maturity. In the latter case the development of the inner organs has been slower in connection with the already initially poor growth rate of the body. On this account the differentiation processes required for maturity have started only at a higher age. With medium growth rate maturity is reached at an intermediate age.

In the two cases with the best and the poorest growth rate the average size at the age of maturity is often relatively small, but higher for a medium growth rate. Yet, in an experiment (year class or population) with good growth rate the average size of the individuals is as a rule greater than in cases with poor growth rate. In populations in which the growth rate is good during the very first years in order later to drop considerably for one reason or another (esp. certain forms or species of whitefish with not genetically determined age for maturity) acceleration of the metabolic processes can bring out maturity at a relatively low age and small size.

Probably also environmental conditions, especially temperature, can exert a certain influence upon the age for maturity. High temperature then produces a lower, low temperature a higher age for maturity.

4. The frequently occurring statements in literature about a decreasing of the growth rate by the process of maturation have been discussed. On the basis of the experiments this has been shown not to apply to wild living fishes in any higher degree. The specimens that on account of better growth rate had reached maturity at the lowest age have not exhibited a growth rate which was poorer than that of the specimens with later maturity which had spawned a lesser number of times than the former.

It has furthermore been shown that in a certain experiment the early mature specimens were as a rule such as had shown a good growth rate throughout their life, while specimens that became mature first at a high age had usually had a poorer growth rate not only from the start, but also in the continuation. The question has been left open, whether

this had been genetically determined or depended on environmental conditions like competition for food, etc.

5. A review has finally been devoted to the reports in literature about higher mortality in males compared with females and about the longevity of fishes in general in connexion with maturity. Also here the results of the experiments have shown that often such reports are inconsistent with facts. Thus the earlier or later age for maturity has not had any perceptible influence on mortality and longevity, and in spite of the fact that the males practically always reach maturity one or two years before the females, mortality has not been perceptibly higher in the former than in the latter. Also at a high age, viz. 9 years for perch and 10 years for trout, the sex ratio has been about 1 : 1.

The known circumstance that in the catches of older and larger specimens in nature the females are as a rule relatively commoner than the males depends with all certainty on the fact that the males are more active than the females. On this account a greater number of them is caught already at lower age, and they are also more exposed to the attacks of predators.

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Observations on the Effect of Rotenone Emulsives on Fish Food Organisms

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Introduction

Rotenone is found in species of *Derris* (tuba root, Malaya and the East Indies), *Lonchocarpus* (cubé or timbo, South America), and many other plants of the family *Leguminosae*. The root has been used by the natives as a fish poison, by the Chinese also as an insecticide.

DURHAM (1903), working in the Federated Malay States, commenced a series of experiments with tuba as a larvicide, and found that *Culex* larvae were killed in 1:40,000 suspension of the dried powdered crude root of *Derris elliptica*. DURHAM also found that the animals most sensitive to tuba are perhaps the Daphnids, and that water-snails are easily killed by the poison.

DANIELS (1905) used crushed fresh tuba (*Derris elliptica*) root to destroy mosquito larvae. He also found that amoebae, rotifers, nematode larvae and the smaller nematodes are completely destroyed by the poison.

HOWARD (1910) reports that decoctions and emulsions of *Derris uliginosa* have considerable potency as larvicides against mosquitoes. Campbell (1916) found that a solution of 1:10,000 killed mosquito (*Stegomyia*) larvae.

In 1926, CASTILLO, investigating the insecticidal properties of three species of *Derris*, found the most effective concentration to be 3 grams of *Derris* powder to 1000 cc. of water, and that *D. polyantha* was the best in killing mosquito larvae. KELSALL et al. (1926) found that a concentration of 10 ppm. derris powder killed mosquito larvae in 3 or 4 days. TWINN (1927) used derris powder in a concentration of 1½ lbs/acre in mosquito control work.

SCHEURING and HEUSCHMANN (1935) found that a concentration of 1:50,000 of finely ground derris killed *Chironomus* in one to several hours; *Daphnia* required 1½ to 4 hours to die in a concentration of 5 ppm.

LEONARD (1939) tested various evertbrates by placing them in a concentration of 1.0 ppm. of powdered derris. None of his test animals showed the slightest sign of distress after being kept in the test solution for 96 hours.

It is not possible to make a reliable comparison between the results of these early investigations; the rotenone content of *Derris* root has been found to vary from 0 to 5½ per cent by ROARK (1931), and of cubé from 8 to 11 per cent by METCALF (1955). About 20 years ago, however, the rotenone content of the commercial derris powder was standardized to 5 per cent.

FELLTON (1940) used 6 and 10 ppm. derris (5 per cent rotenone) to kill mosquito larvae in midge control work. HAMILTON (1941) tested various concentrations of derris on fresh-water animals and found the lethal concentration for some evertebrates to be: 0.5 ppm. for cladocers and copepods, 2 ppm. for leeches, and 10 ppm. for amphipods and *Planaria*. SMITH (1941) treated Potter's Lake, New Brunswick, with a concentration of 0.5 ppm. derris, and found that planktic microcrustaceans, *Chaoborus* larvae, a snail, and one species of leech were killed. BROWN and BALL (1943) report that after the treatment of Third Sister Lake with 0.5 ppm. derris, *Peridinium*, *Daphnia*, and *Diatomus* disappeared, rotifers were reduced. *Cyclops* showed a sharp decline, and aeschnine dragonflies, leeches, and *Chaoborus* were seriously affected by the poison. HOOPER (1948) found that the treatment of Demming Lake, Minnesota, with 0.5 ppm. of derris killed all the cladocers and copepods. The effect of the poisoning of Smith Lake, Northern Colorado, with 1.0 ppm. derris upon the macroscopic bottom fauna was studied by CUSHING and OLIVE (1956) and upon plankton by HOFFMAN (1956). CUSHING and OLIVE found that the majority of the tendipedids collected 3 days after poisoning were dead; and HOFFMAN found that the numbers of *Ceratium* and *Entomostraca* dropped to zero after the treatment, and that the rotifer population was reduced.

The treatment of fresh-water habitats with powdered derris has been more and more replaced by poisoning with various rotenone emulsives. The rotenone emulsives are more easily dispersed in the water than are the powders, and they are also less irritating to human eyes and mucous membranes. As the rotenone emulsives have greater capacity for penetrating thermally stratified bodies of water and also the littoral zone of rooted vegetation, they affect the bottom and littoral organisms to a higher extent than do the derris powders. The adding of a synergist in some of the emulsives increases their poisonous effect.

The toxic effect of the rotenone emulsives is higher in acid waters than in alkaline (ÖBERG, 1956). BERZINS (1958) found that a concentration of 0.4—0.5 ppm. of the synergized rotenone emulsive Pro-Noxfish was enough to kill practically all animals in two small lakes with pH about 6 in Southern Sweden. Only a few evertebrates of the epiphyton and bottom fauna survived the treatment.

A very valuable review of rotenone and its use in fisheries research is given by KRUMHOLZ (1948).

The author has studied the effects of rotenone emulsives upon fish food organisms in connection with fish-poisonings in three lakes in Central Sweden. The poisonings were carried out during summer and fall 1958. Most of the organisms observed during these studies proved to be affected by the rotenone emulsives. In connection with the poisonings in one of these lakes, Lake Erken, laboratory and field experiments on some of the macro-

scopic bottom animals were carried out by LINDGREN (1959). He found that the test animals were adversely affected by concentrations of about 1 ppm. of the rotenone emulsives.

The Local Poisonings in Lake Erken

During summer and fall, 1958, a series of local poisonings with rotenone emulsives were carried out in small creeks of Erken by fil. mag. Thorsten Anderson for fish population studies. During 18 of these operations the effect of the drugs on plankton and littoral organisms was studied.

The investigation was planned by Professor Wilhelm Rodhe, Institute of Limnology, Uppsala University. By his great interest in the subject, his encouragement and suggestions in the course of the work, Professor Rodhe has been of the greatest help for the carrying out of this study.

Lake Erken is a naturally eutrophic lake situated 50 kilometers east of Uppsala. Its surface area is 23 km². The creeks, in which the experiments were conducted, have a vegetation of *Phragmites*, or *Phragmites* mixed with *Scirpus*. Their pH varied from 8.2 to 8.5. The bottom of the creeks is commonly clay covered by a thin layer of sand. The shores of some creeks are more or less stony.

Various concentrations of the rotenone emulsives were tried in the experiments, ranging from 0.5 to 4.5 ppm. In the first 5 of these poisonings, Chem Fish Special (containing 5 per cent rotenone and 11 per cent other Cubé extractives) was used, in the following treatments Pro-Noxfish (2.5 per cent rotenone, 5 per cent other Cubé extractives, and 2.5 per cent "Sulfoxide" (cf. METCALF, 1955)) was used. The toxicants were injected into the water at different depths, and/or sprayed over the surface with the help of a hand spray. Qualitative plankton net samples, bottom, and periphyton samples were collected before and one to several times after each poisoning. The collections made before poisoning were used as controls.

The poisonings were carried out under various weather conditions, but as a rule when inshore wind was blowing. It is always difficult to get the poison evenly dispersed in a body of water, and in local poisonings such as those described in the present paper it is even more so, as new water masses containing unaffected organisms enter the poisoned area all the time during the experiments. The concentrations of the rotenone could therefore be only very roughly estimated, and only the immediate effect of the toxicant on the organisms was indicated. The first fish came to the surface of the water about 15 minutes after the poisoning. Among the fish food organisms, only some of the microcrustaceans responded to the drugs within the same time as did the fishes, other organisms required 2 to 8 hours or more before they showed any sign of distress.

The Poisoning of Salbosjön

Salbosjön (Salbo Lake) was treated totally on August 24, 1958. The poisoning was carried out by Fishery Inspector Arne Andersson, Norrtälje.

Salbosjön is a small bog-lake with brown water and dy bottom, situated 50 kilometers north-east of Uppsala. Its surface area is 20,000 m², the mean depth 2 meters. The pH is 7.5. The rooted vegetation of the shore is very scanty and consists mostly of *Equisetum*, *Scirpus* and some *Nuphar*.

Sufficient Pro-Noxfish to make a concentration of 0.6—0.7 ppm. was added to Salbosjön on August 24, 1958. The poisoning was carried out from two row-boats, one equipped with the same hand spray as used in the Erken experiments; the other with a spray permitting the drug to be spread over the surface of the water but not to be injected under the surface. The weather seemed to be favorable, the day being cloudy, and the temperature of the water 17°C. The boats were rowed in straight lines crossways over the lake. The rooted aquatic vegetation was treated with very turning of the boats.

Plankton net samples were taken before and after the poisoning from the middle of the lake and from the littoral zone. The samples were examined immediately after collecting.

The Poisoning of Halmsjön

In order to eradicate the fish population, Halmsjön (Halm Lake) was treated totally on July 10, 1956, and again from November 17 to November 22, 1958. The poisonings were carried out by the Institute of Fresh Water Research, Drottningholm.

Halmsjön is a naturally eutrophic lake, very little influenced by civilization (PEJLER, 1957). The lake is situated 30 kilometers south of Uppsala. Its surface area is 0.38 km², the maximum depth 5 1/2 meters. The lake is surrounded by *Phragmites*. The belt of submersed rooted vegetation is very broad, especially in the western part of the lake.

On July 10, 1956, 600 liters of Pro-Noxfish were applied to Halmsjön, sufficient to give a concentration of 0.5 ppm. Water temperature at the time of the poisoning was 20°C, and the day was sunny. The operation was not successful: pike, perch and roach survived the treatment. No collections of fish food organisms were taken in connection with this poisoning.

For the second application, from November 17 to November 22, 1958, 682 liters of Pro-Noxfish were used, giving a concentration of 0.5—0.6 ppm. The water temperature at Nov. 17 was 5°C, the pH 7.4. The treatment was carried out in four stages, the free water surface being sprayed with the toxicant on Nov. 17, the belt of rooted littoral vegetation on Nov. 18, and the inflows on Nov. 19 and 22.

Plankton net samples were collected before and after the treatment and examined immediately after collecting. Quantitative plankton samples were collected before and after the poisoning with a 5 liter plankton sampler (RODHE, 1941) at different stations and depths of the lake and counted in Utermöhl chambers with inverted microscope (UTERMÖHL, 1958).

The plankton samples taken before the 1958 poisoning contained, with few exceptions, the same species as were found by PEJLER 1955,¹ one year before the first poisoning (PEJLER, 1957).

Observations on Plankton Algae

Volvox aureus. — This species appeared to be affected only where the concentration of the rotenone emulsives was calculated to 2 ppm. or more. These strong concentrations caused the death of all colonies in the samples within 2 hours after poisoning. The rolling movements of the colonies were gradually slowed and finally stopped at the same time as some of the colonies were seen to burst.

Synura. — In samples taken immediately after the treatment of Salbosjön a few colonies died within 20 minutes after collecting, but most colonies survived and were apparently unaffected by the drug. The reaction of *Synura* to the poison was a gradual slowing of movements until the colonies lay quietly on the bottom of the dish.

Uroglena. — In surface samples taken 2 hours after the poisoning of the surface of Halmsjön, only a few *Uroglena* colonies were still alive. These colonies died within a few minutes after collecting. 3 and 5 meter samples collected 2 hours after the poisoning contained only unaffected colonies. No samples collected later that day contained any living *Uroglena* colony. The action of rotenone on *Uroglena* was similar to its action on *Synura*: a gradual slowing of the movements of the colonies until they sank to the bottom of the dish.

Peridinium. — In most collections from Erken, *Peridinium* seemed to be unaffected by the poison. The action of rotenone on *Peridinium* was a gradual slowing of the ciliar movements which caused the cells to sink to the bottom.

Ceratium hirundinella. — *Ceratium* seems to be more sensitive to rotenone than *Peridinium*. An estimated concentration of 1.0 ppm. of the rotenone emulsives killed 100 per cent of the cells within 4 hours after the poisoning. No living *Ceratium* was found neither in Salbosjön nor Halmsjön in samples collected after the poisoning. The poison caused a gradual slowing of the ciliar movements accompanied by the sinking of the cells.

¹ Dr Birger Pejler at the Institute of Zoology, Uppsala, has kindly lent me his plankton collections from Halmsjön for comparison.

Observations on Invertebrates

Protozoa. — The protozoa seemed to be little affected by the poisonings in Erken. Living planktic ciliates, living benthic ciliates, and living techa-moebae were found in most samples. Hypotrich ciliates were all dead in a bottom sample taken 23 hours after a treatment with 1.5 ppm.

Hydra vulgaris was found in epiphyton samples taken 3 hours after treatment with 2 ppm. In these samples, which were examined 3 hours after collecting, all specimens of *Hydra* were found to be dead, lying in a relaxed condition.

Plathyhelminthes. — Living cercariae were found in both plankton and benthos samples taken after poisoning in Erken. In an epilithon sample collected after a treatment with about 4.5 ppm. Pro-Noxfish, 50 per cent of the cercariae died within 7 hours after poisoning. Specimens of *Planaria* found in the same sample were all dead. *Stenostomum sp.* was killed within 4 1/2 hours after treatment with about 0.6 ppm. Chem Fish Special. Other small turbellariae found in periphyton and bottom samples in Erken were all unaffected by the poisonings.

Gastrotrichs in bottom samples from Erken were not affected by the rotenone. In an epilithon sample (about 4.5 ppm.) 25 per cent of the animals died within 7 hours after poisoning.

Rotatoria. — No specimen of *Brachionus* was found in samples from Halmsjön after poisoning, although the quantitative samples taken before poisoning contained a small number of this species. Bdelloid rotifers present in bottom and periphyton samples from Erken were all dead within 6 1/2 hours after the poisoning. In Erken *Keratella cochlearis* was completely killed only where the concentration was estimated to 1.0 ppm. or more. No living specimen of *Keratella cochlearis* was found in samples from Salbosjön after poisoning. Surface samples taken immediately after the poisoning of the surface of Halmsjön contained no living *Keratella cochlearis*; the 3 meter samples contained only a few dead *Keratella*, the majority of these animals being still unaffected by the drug. The quantitative samples from Halmsjön collected 3 and 10 days after the poisoning contained living *Keratella cochlearis* and *Keratella quadrata*. In samples from Erken, *Keratella quadrata* was killed within 4 to 5 hours after poisoning. *Keratella hiemalis* was found in some of the samples taken in Halmsjön before poisoning, but no specimen was found in the samples collected after poisoning.

In the Erken experiments the minimum time required to give a 100 per cent kill of *Kellicottia longispina* in an estimated concentration of 0.5 to 0.6 ppm. was 7 hours, in 2 ppm. 4 hours. Living specimens were found in the quantitative samples collected after the poisoning of Halmsjön.

In most of the Erken experiments *Euchlanis dilatata* was killed within 4 to 8 hours after the poisoning. No living *Euchlanis dilatata* was found in

samples from Salbosjön collected later than 2 hours after the poisoning. 25 per cent of the *Euchlanis incisa* was killed within 6 1/2 hours after the treatment with about 1 ppm. in Erken.

In most of the Erken experiments the *Trichocerca* spp. required 8 hours to give a 100 per cent kill. In an estimated concentration of 4.5 ppm. they died within 4 1/2 hours after the treatment. No living *Trichocerca* was found in collections from Salbosjön or Halmsjön after poisoning.

Gastropus stylifer was alive in surface samples collected in Halmsjön 2 hours after the poisoning. No *Gastropus* was found in samples collected later than 2 hours after the poisoning. *Ascomorpha saltans* in samples from Erken was killed within 6 hours after the treatment with about 1 ppm. In samples collected 2 hours after treatment of Salbosjön and Halmsjön, 50 per cent of the *Ascomorpha* spp. were found dead. Collections made later than 2 hours after the poisonings contained no *Ascomorpha*.

In Erken *Asplanchna priodonta* was completely killed within 5 hours after poisoning with Chem Fish Special. In those Erken experiments where Pro-Noxfish was used, no *Asplanchna* was killed. No living *Asplanchna* was, however, found in samples taken after the poisoning of Salbosjön. In Halmsjön, the *Asplanchna* population was reduced by about 50 per cent within 10 days after the poisoning. *Synchaeta pectinata* and *Synchaeta grandis* were both strikingly similar to *Asplanchna* in their reactions to the rotenone emulsives, for both were completely killed by Chem Fish Special but appeared to be unaffected by Pro-Noxfish in the Erken experiments. In Halmsjön, however, no living *Synchaeta* was found in samples collected after the poisoning.

In Erken all *Polyarthra* spp. were killed within 4 to 8 hours after the poisoning. The quantitative samples collected 3 days after the treatment of Halmsjön contained a few individuals of *Polyarthra vulgaris* and *Polyarthra dolichoptera* but no *Polyarthra euryptera*. *Polyarthra* were completely absent in samples taken 10 days after the poisoning.

Living *Pompholyx sulcata* was present in samples collected before the treatment of Halmsjön and also in samples collected 2 hours after the poisoning of the surface. Samples collected later than 2 hours after the treatment contained no *Pompholyx sulcata*. The qualitative samples collected in Halmsjön after poisoning contained no living *Filinia longiseta*. The quantitative samples taken 3 days after the treatment contained a few individuals, those collected 10 days after the poisoning, however, contained no *Filinia*.

Conochilus hippocrepis appeared to be little affected by concentrations weaker than 1.0 ppm. in the Erken experiments. In 1.0 ppm. all colonies were dead within 4 hours after the poisoning. In Salbosjön they were all active in samples taken 2 hours after poisoning. All specimens of *Conochilus unicornis* found in the qualitative samples collected in Halmsjön 2 and

4 hours after the surface-poisoning were active and apparently unaffected by the drug. The quantitative samples collected 3 days after poisoning contained a few colonies of *Conochilus unicornis*, those taken 10 days after poisoning none.

Proales sordida was killed within 7 hours after the poisonings in Erken collections.

The action of rotenone on all these rotifers was a gradual slowing of movements, followed by complete narcosis and death. All dead individuals lay with their body relaxed. The movements of surviving individuals appeared quite normal.

Nematodes. — The epiphyton samples collected on *Phragmites* and *Scirpus* in Erken contained many small nematodes. In samples taken 23 hours after the poisonings 25 to 50 per cent of these animals were found to be dead. In an estimated concentration of 4.5 ppm. 50 per cent of the nematodes were killed within 6 1/2 hours after poisoning.

Oligochaeta. — Both HOOPER (1948) and CUSHING and OLIVE (1956) found an increase in the oligochaete population after poisoning with derris powder in concentrations of 0.5 and 1.0 ppm. respectively. This increase may be due to the relative tolerance of most species of oligochaetes to rotenone. In Erken concentrations weaker than 1.5 ppm. had no apparent effect on *Chaetogaster*. 100 per cent of these animals were killed within 7 hours after treatment with an estimated concentration of 2 ppm., and in about 4.5 ppm. they were killed within 4 hours after the poisoning. The naidids were more sensitive to the toxicants than was *Chaetogaster*. 100 per cent of the naidids died within 5 hours after treatments with concentrations ranging from 0.5 to 2 ppm. In Erken *Stylaria lacustris* appeared to be unaffected by Pro-Noxfish and weaker concentrations of Chem Fish Special. In periphyton samples collected after treatments with about 1 ppm. Chem Fish Special all *Stylaria* were killed within 5 hours after the poisoning.

Hirudinea. — In a bottom sample taken after treatment with an estimated concentration of 2 ppm. all *Proclipsis tessellata* and the smaller individuals of *Herpobdella octoculata* were killed within 8 hours after the poisoning. The larger specimens of *Herpobdella* all survived the treatment.

Cladocera. — No *Sida crystallina* was found in collections from the weaker concentration experiments in Erken. In about 1 ppm. 100 per cent of these animals were killed within 2 hours after the poisoning. No living *Diaphanosoma brachyurum* was recovered in collections taken after the poisonings.

In Erken *Daphnia spp.* were active in samples collected within one hour after treatment with 0.6 ppm. In all other collections taken after poisoning during the Erken experiments the recovered *Daphnia* specimens were dead. Samples taken after the poisonings of Salbosjön and Halmsjön contained no living *Daphnia*.

No *Scapholeberis mucronata* or *Acroperus harpae* survived in any sample collected after poisonings in Erken. *Ceriodaphnia* spp. gave a 100 per cent kill after the treatments in all three lakes. No living *Bosmina coregoni* was recovered in samples collected after poisoning in Erken and Salbosjön. It is, however, delicate to estimate to what degree this cladocer was affected by the rotenone, for *Bosmina* is very sensitive to net-sampling and was often found dead in the controls. Anyhow, the quantitative samples collected in Halmsjön 3 days after poisoning contained no *Bosmina*, nor did the samples taken in Salbosjön 1 week after poisoning.

In the Erken experiments *Peracantha truncata* was killed within 2 hours after poisoning, unidentified cladocer larvae within 3 hours, *Leptodora kindti* also within 3 hours, and *Polyphemus pediculus* within 5 hours. Only dead or dying specimens of *Leydigia leydigii* were found in plankton and periphyton samples collected after poisoning in Erken, but the quantitative samples taken close to the bottom in the outer littoral zone of Halmsjön contained living *Leydigia* 3 days after poisoning.

The *Alona* spp. were not affected by concentrations ranging from 0.5 to 1.0 ppm.; an estimated concentration of 4.5 ppm. gave a 100 per cent kill within 7 hours. *Alonella excisa*, in epiphyton samples, was killed within 8 hours in about 1.5 ppm., and within 5 hours in about 4.5 ppm. *Alonella nana* was apparently not affected by the rotenone emulsives in the Erken experiments. Living specimens were also found in the quantitative samples collected in Halmsjön 3 days after poisoning.

Pleuroxus uncinatus was apparently not affected by the weaker concentrations of the toxicants. In an estimated concentration of 2 ppm. it was killed within 5 hours after poisoning. The quantitative samples collected after the poisoning of Halmsjön contained no *Pleuroxus*. *Chydorus* spp. were mostly unaffected by the weaker concentrations of the toxicants in the Erken experiments; in the stronger concentrations they were killed mostly within 5 hours after poisoning.

Copepoda. — In Erken all *Diaptomus graciloides* were found dead in samples collected after poisoning. This species is, however, sensitive to net-sampling, and was as a rule also found dead in the controls. In samples collected before the treatment of Salbosjön, all *Diaptomus* specimens were alive, but samples collected after poisoning contained no living individual. Adults, copepodites, and metanauplii of *Diaptomus gracilis* were all alive in samples collected before the treatment of Halmsjön. Samples collected after the poisoning contained no *Diaptomus*.

Adults of *Eurytemora velox* were all alive and apparently unaffected in samples collected after treatment with about 0.6 ppm. Chem Fish Special. In all other samples collected after poisoning during the Erken experiments

the *Eurytemora* adults were killed within 8 hours after poisoning. *Cyclops* spp., found in Erken samples, were mostly killed within 5 to 6 hours after poisoning. Only a few specimens of *Cyclops* survived the treatment of Salbosjön; no living *Cyclops* was, however, found in samples collected after the poisoning of Halmsjön. The harpacticides recovered in net samples from Erken appeared to be unaffected by the toxicants. In epiphyton samples they were killed within 23 hours after treatment with an estimated concentration of 0.5 ppm. and within 5 hours in 2 ppm.

Ostracoda. — Ostracods found in net samples from Erken were all alive and seemed to be unaffected by the poison. In bottom samples 25 per cent of the ostracods were killed within 5 hours after treatment with an estimated concentration of 0.5 ppm., and 100 per cent within 2 hours after treatment with about 2 ppm. In epiphyton samples the ostracods were killed within 23 hours in an estimated concentration of 0.5 ppm.

Hydrachnidae. — During the Erken experiments the hydrachnids were apparently not affected by concentrations ranging from 0.5 to 1.5 ppm. All adult hydrachnids and hydrachnid larvae were found dead 23 hours after treatment with an estimated concentration of 2 ppm. The hydrachnid larvae may be more sensitive to rotenone than are the adults, since in 1.0 ppm. 75 per cent of the hydrachnid larvae were killed within 23 hours after poisoning, but all adults seemed to be unaffected by the treatment.

Insecta. — In Erken *Caenis* was apparently not affected by concentrations estimated to 2 ppm. of Pro-Noxfish, but other unidentified ephemeropterid larvae were all killed within 7 hours after treatment with the same concentration.

Campedioid trichopterous larvae were all killed within 5 hours after poisoning with an estimated concentration of 1.0 ppm. in Erken. The eruciform trichopterous larvae, however, seemed to be unaffected by the treatment in concentrations weaker than 1.5 ppm., in 2 ppm. they were all killed within 8 hours.

The ceratopogonid larvae (*Palpomyia* and *Bezzia*) seemed to be unaffected by the weaker concentrations of the rotenone emulsives in the Erken experiments. In an estimated concentration of 2 ppm. they were all killed within 8 hours after poisoning, and in 2.5 ppm. within 4 hours. Small chironomid larvae in epiphyton and periphyton samples from Erken were all killed within 23 hours after treatment with 0.6 ppm. or more.

A great number of adult *Gerris* and *Gyrinus* were travelling over the surface of Salbosjön before poisoning. Their numbers were apparently not reduced by the treatment.

Mollusca. — 50 per cent of the small planorbids of the epiphyton were killed within 7 hours after the treatment with an estimated concentration of 1.5 ppm. Pro-Noxfish, and *Theodoxus fluviatilis* was killed within 8 hours in 2 ppm.

Table 1. Plankton of Salbosjön before and after poisoning with Pro-Noxfish (from net plankton samples).

Organism:	Before poisoning	After poisoning	
	24/8	31/8	14/9
<i>Volvox</i>	+++	++	++
<i>Synura</i>	++	++	+++
<i>Ceratium hirundinella</i>	+++	—	—
<i>Halteria</i>	—	—	+
<i>Paramecium</i>	—	—	+
<i>Stentor polymorphus</i>	+	+	+
<i>Vorticella</i>	+	—	+++
<i>Keratella cochlearis</i>	++	—	—
<i>Euchlanis</i>	+	—	—
<i>Trichocerca</i>	+	—	—
<i>Ascomorpha</i>	+	—	—
<i>Asplanchna priodonta</i>	+	—	—
<i>Conochilus hippocrepis</i>	+	—	—
<i>Daphnia</i>	+	—	—
<i>Ceriodaphnia quadrangula</i>	++	—	—
<i>Diaphanosoma brachyurum</i>	+	—	—
<i>Bosmina</i>	+	—	—
<i>Alona</i>	—	—	+
<i>Diaptomus</i>	+++	—	—
<i>Cyclops</i>	+++	+	+
<i>Copepodites, Cyclops</i>	+	—	—
<i>Metanauplii</i>	++	—	—
<i>Nauplii</i>	+	—	—

Conclusions

Even when using the same rotenone preparation and the same concentration, the result of the treatment on the organisms will vary a great deal. There are many factors influencing the toxic effect of the rotenone. Its toxicity is decreased by exposure to light, oxygen, alkali, heat and turbidity. BERZINS (1958) reports, as already stated (p. 147), that all planktic and most of the bottom and epiphyton animals were killed after treatments with 0.4—0.5 ppm. in two lakes with pH about 6. In Salbosjön, where the pH varies about 7.5, all rotifers and *Ceratium hirundinella* were killed by a concentration of 0.6—0.7 ppm. (Table 1). Of the microcrustaceans only *Alona* and a few *Cyclops* survived the treatment. In Halmsjön, where the pH varies about 7.4, some of the planktic rotifers and a few microcrustaceans survived the treatment (Table 2). In Table 3, the organisms are arranged according to their sensibility to the toxicants, as observed during the Erken experiments.

The concentrations most used in fish eradicating works, 0.5—0.6 ppm., are strong enough to kill most of the planktic animals and also some of the bottom and epiphyton forms. The planktic cladocers are very sensitive to the rotenone, most of them showing toxic effects already within $\frac{1}{4}$ hour after poisoning and giving a 100 per cent kill within 3 hours. It is remarkable that the planktic species of *Chydorus* are more tolerant to the rotenone than

Table 2. Zooplankton of Halmsjön before and after poisoning (from plankton trap samples), expressed in individuals per liter.¹

Zooplankton:	Before	After poisoning	
	17/11	20/11	27/11
<i>Brachionus</i> sp.	+	—	—
<i>Keratella cochlearis</i>	74	2	2
<i>Keratella quadrata</i>	+	+	+
<i>Keratella hiemalis</i>	+	—	—
<i>Kellicottia longispina</i>	3	+	+
<i>Trichocerca porcellus</i>	1	—	—
<i>Trichocerca capucina</i>	+	—	—
<i>Trichocerca</i> sp.	+	—	—
<i>Gastropus stylifer</i>	4	—	—
<i>Ascomorpha</i> sp.	+	—	—
<i>Ascomorpha saltans</i>	+	—	—
<i>Asplanchna priodonta</i>	5	4	2
<i>Synchaeta</i> spp.	1	—	—
<i>Polyarthra vulgaris</i>	9	+	—
<i>Polyarthra dolichoptera</i>	1	+	—
<i>Polyarthra euryptera</i>	6	—	—
<i>Pompholyx sulcata</i>	2	—	—
<i>Filinia longiseta</i>	22	+	—
<i>Conochilus unicornis</i>	10	+	—
<i>Daphnia cucullata</i>	1	—	—
<i>Ceriodaphnia quadrangula</i>	+	—	—
<i>Ceriodaphnia setosa</i>	+	—	—
<i>Bosmina coregoni</i>	1	—	—
<i>Alonella nana</i>	+	+	—
<i>Pleuroxus uncinatus</i>	+	—	—
<i>Leydigia leydigii</i>	—	+	—
<i>Chydorus sphaericus</i>	+	+	+
<i>Diaptomus gracilis</i>	8	—	—
<i>Copepodites, Diaptomus</i>	2	—	—
<i>Metanauplii, Diaptomus</i>	+	—	—
<i>Nauplii, Diaptomus and Cyclops</i>	+	—	—
<i>Metanauplii, Cyclops</i>	+	—	—
<i>Copepodites, Cyclops</i>	+	—	—
<i>Cyclops, adults</i>	1	—	—
Number of species	28	11	5

¹ Number of individuals less than 5 per 5 liters is indicated by a + sign.

other planktic cladocers, being mostly unaffected by treatment with 0.5—0.7 ppm. (Table 2 and 3); they required a concentration of 1.0 ppm. to give a 100 per cent kill, and up to 5 hours to succumb in this concentration. The periphytic and bottom cladocers were not so easily killed as the planktic ones, they required as a rule stronger concentrations and longer time to give a 100 per cent kill: thus *Alonella excisa* was killed by 100 per cent only within 8 hours in a concentration of 1.5 ppm., *Pleuroxus uncinatus* within 5 hours in 2 ppm., and the *Alona* spp. by 100 per cent only in a concentration as strong as 4.5 ppm. It is very likely that the detoxifying influences of the biotopes increase the chances for these bottom and epiphytic forms to survive the poisoning.

Table 3. Sensibility of various organisms to rotenone emulsives according to observations in Lake Erken.

Estimated concentration:	Time in hours required to give a 100 %/o kill:
0.5—0.6 p p m. (Pro-Noxfish and Chem Fish Special):	
<i>Diaphanosoma brachyurum</i>	0.5—1.5
<i>Daphnia</i> spp.	2
<i>Scapholeberis mucronata</i>	2
<i>Peracantha truncata</i>	2
<i>Cladocer</i> larvae	3
<i>Leptodora kindti</i>	3
<i>Ceriodaphnia</i> spp.	3
<i>Synchaeta</i> spp.	4 (only in Chem Fish Sp.)
<i>Keratella quadrata</i>	4—5
<i>Leydigia leydigii</i>	4—5
<i>Stenostomum</i> sp.	4.5
<i>Euchlanis dilatata</i>	4—8
<i>Polyarthra</i> spp.	4—8
<i>Asplanchna priodonta</i>	5 (only in Chem Fish Sp.)
Naidids	5
<i>Polyphemus pediculus</i>	5
<i>Acroperus harpae</i>	5
<i>Cyclops</i> spp.	5—6
<i>Bdelloid rotifers</i>	6.5
<i>Kellicottia longispina</i>	7
<i>Proales sordida</i>	7
<i>Trichocera</i> spp.	8
<i>Eurytemora velox</i>	8 (only in Pro-Noxfish)
<i>Chironomid larvae</i>	23
1.0 p p m. (Pro-Noxfish and Chem Fish Special):	
<i>Ceratium hirundinella</i>	4
<i>Conochilus hippocrepis</i>	4
<i>Keratella cochlearis</i>	4
<i>Chydorus</i> spp.	5
<i>Campedioid trichopterosus larvae</i>	5
<i>Stylaria lacustris</i>	5 (only in Chem Fish Sp.)
<i>Ascomorpha saltans</i>	6
1.5 p p m. (Pro-Noxfish):	
<i>Alonella excisa</i>	8
<i>Hypotrich ciliates</i>	23
2.0 p p m. (Pro-Noxfish):	
<i>Volvox aureus</i>	2
<i>Pleuroxus uncinatus</i>	5
<i>Chaetogaster</i> spp.	7
<i>Ephemeroid larvae</i>	7
Small leeches	8
<i>Eruciform trichopterosus larvae</i>	8
<i>Ceratopogonid larvae</i>	8
<i>Theodoxus fluviatilis</i>	8
<i>Hydrachnidae</i>	23
4.5 p p m. (Pro-Noxfish):	
<i>Planaria</i> sp.	7
<i>Alona</i> spp.	7

Most of the rotifers were killed by concentrations of 0.5—0.6 ppm. although they required a longer time to give a 100 per cent kill than did the cladocers, as a rule between 4—8 hours. It is interesting that the *Synchaeta spp.* and *Asplanchna priodonta* during the Erken experiments were killed only by Chem Fish Special, but appeared to be unaffected by treatments with Pro-Noxfish. Also in Halmstön about 50 per cent of *Asplanchna priodonta* survived the treatment (Table 2). *Conochilus*, *Keratella* and *Ascomorpha* showed, during the Erken experiments, to be more tolerant to the rotenone than other rotifers. they were killed by 100 per cent only in a concentration of 1.0 ppm.

Stenostomum and the naidids showed to be well as sensitive as the most sensitive rotifers, giving a 100 per cent kill within 4.5 hours in 0.5—0.6 ppm.

Cyclops spp. and *Eurytemora velox* were killed by 0.5—0.6 ppm., the former within 5—6 hours, the latter within 8 hours. It is, however, remarkable that *Eurytemora* was killed by 100 per cent only where Pro-Noxfish was used.

The chironomid larvae were also totally killed in 0.5—0.6 ppm., they required however 23 hours for a 100 per cent kill. The campediod trichopterous larvae and *Stylaria lacustris* were both killed within 5 hours after treatment with 1.0 ppm., *Stylaria*, however, showed a 100 per cent kill only where Chem Fish Special was used.

Volvox aureus, which was unaffected by the weaker concentrations, was totally killed within 2 hours in 2 ppm. This concentration also killed most of the bottom animals within 7—8 hours, and hydrachnids within 23 hours (Table 3).

It is, however, to be pointed out, that the figures given above are only preliminary, but it is evident that most of the zooplankton, much of the bottom and epiphyton fauna, and some of the phytoplankters are killed by treatments with rotenone emulsives in concentrations used to eradicate fish.

Summary

During summer and fall 1958, the effect of rotenone emulsives upon fish food organisms was studied in connection with fish poisoning in three lakes in Central Sweden. Most of the zooplankton, much of the epiphytic and bottom animals and some of the phytoplankters were totally killed by 0.5—0.6 ppm., the concentration generally used in fish eradicating.

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Observations on the Age of Fishes¹

By HANS HEDERSTRÖM

HEIBRUN's pike with a length of 9¹/₂ ells (c. 565 cms.), a weight of 17¹/₂ "lispund" (c. 148 kgs.), and an age of 267 years (see *Oeconomisches Lexicon*, heading "Hecht") has always appeared to me something of an exaggeration. Especially its age seemed to be most unbelievable. I thought: Is it in agreement with the order established within the animal kingdom that nobler and more useful animals should have such a short span of life compared with that of the pike? That the pike after having lived 70 or 80 years shall, according to ancient belief, still enjoy the springtime of life, while even man is already wasted?

I do not deny that there exist many things in the mineral and plant kingdom which surpass man with regard to age. An oak, a *Sorbus suecica*, and other trees can reach an age of 4 or 5 generations. But let us cast a look upon the Creator's wise laws in Nature. What is intended to last a long time, has to be accomplished slowly. What grows more slowly than the rock, what is more lasting? What develops more quickly than a fungus, but what is at the same time more perishable? The greater and stronger trees are intended to be used by man for the construction of houses which shall stand against time, of ships which shall withstand the impetuosity of the waves. For this aim slow growth and strong resistance are required. But why should fish, which after all can never serve any other purpose than that of providing a meal, grow for 200 or 300 years?

These and similar thoughts made me disinclined to harbour such high

¹ This remarkable article was published in Swedish in the Transactions (Handlingar) of the Royal Swedish Academy of Science in 1759. The reference to the original thus is: HEDERSTRÖM, H. 1759. Rön om Fiskars Ålder. *Handl. Kungl. Vetenskapsakademien (Stockholm) Vol. XX: 222—229.*

HEDERSTRÖM was a clergyman and parson in the diocese of Linköping in southern Sweden. The article was sent by the Secretary of the Academy to LINNAEUS who recommended its publication, and in a letter pointed out that he himself never came to think of this possibility of working out the age of fishes.

HEDERSTRÖM was awarded a gold medal for his article which, however, remained on the whole unknown in international circles in spite of the fact that it was mentioned in Swedish literature in 1909 in connection with the 150 years' jubilee. From there brief references found their way, e.g. into VAN OOSTEN's paper on growth and age of *Leucisthys* (1929).

On the eve of the bicentenary of the first publication of the article the editors desire to pay homage to this early pioneer by its re-publication *in extenso*, although in modern English so as to make it internationally accessible. In the history of the determination of the age of fishes HANS HEDERSTRÖM will always by sure of a prominent place.

ideas about the presumed age of the pike. Since, however, such thoughts, however probable they may appear, can never bring about a final decision in matters of natural science, I have during several years taken pains to study the age and growth of fishes. In doing so I have experienced great difficulties, as these inhabitants of the wet element hide from man not only their conception, but also their birth and life history. Gradually the thought struck me that perhaps the Creator himself might have inscribed upon these animals some sign to give witness of their age, as it happens so clearly with some other animals. The problem then was to investigate into such a mark or sign. I respectfully leave it to the enlightened scrutiny of the Royal Academy of Science and of all students of natural history to decide to what extent my endeavours may have been successful.

My proposition is that the age of fishes is expressed in their vertebrae in the same way as the age of trees is indicated by the growth rings the number of which agrees with the number of years of age. Anybody who will take the trouble of examining a vertebra of a boiled fish will see some rings upon it. The number of rings expresses the age of the fish in years. It has, however, to be kept in mind that the rings are not as clearly and distinctly visible in fresh condition as when the bones have dried, and also that they are more clearly seen in big fish than in small. When the vertebrae of large fish have been stored and dried for a longer time the rings are distinctly visible, and can be counted with certainty.

The reliable foundation of this age indicator I believe to be demonstrable by the following reasons and circumstances.

1. Either side of a vertebra displays the same number of rings.
2. All vertebrae, both larger and smaller, of one and the same fish have the same number of rings.
3. A large and a small individual of a species of fish have identical numbers of vertebrae, but
4. a very different number of rings, the large individual having upon each vertebra 12, 15, or more rings, while the small fish of the same species has only 2, 3, or more, all according to size and age. I never observed a small fish to have as many, still less more rings than a larger individual of the same species, in spite of the fact I have examined many fish of different sizes, but I have always found the number of rings to be roughly proportionate to the size of the fish.
5. This sign fitted also exactly with fish the age of which was previously known either from experience or from other circumstances.
6. An examination of a vertebra and of the position of its rings leads to the conviction that their growth is brought about by accrescence, from the marrow obliquely in peripheral direction, and that it thus increases not only the length but also the girth of the fish. The outermost rings are mostly softer, darker, and thinner than the others, subsequently they become as hard

as cartilage, and finally as hard as bone. As long as the growth of these outermost rings continues the fish is not full-grown, but when the outermost rings do no longer show this condition but are as hard as the others, the fish has probably reached its full size.

Nobody would demand an exact similarity of all fishes of the same species and the same size. Neither are human beings and other animals of identical age always of the same size. Some difference in fishes can result from more or less refreshing water, but also from more or less abundant food. In large lakes with many in- and outlets, or where there is a current of water the fish thrive and grow better than in small marshy pools. Also low shores with plenty of vegetation contribute to the well-being of the fish. Perch, eel, and burbot thrive, where there is abundance of smelt, and bleak, and where there is plenty of perch and roach the pike finds an abundant table, grows, and reaches a large size.

According to this principle I have examined the age of several kind of fish. I only want to mention the best known, like pike, perch, roach, bream, chub, codfish, eel, burbot, etc., which all bear witness to the correctness of my sign. From this I have drawn the conclusion that a pike, the size of a normal Baltic herring with a weight of 3 or 4 "lod" (c. 40 or 55 gms.) is 1 year old. One of the length of 1 1/2 or 2 "kvarter" (c. 23 or 30 cms.), of the size of a normal herring, which weighs 7—8 "lod" (c. 95—120 gms.) is 2 years old. One of the length of 3 "kvarter" (c. 45 cms.), which weighs about 1 "mark" (c. 425 gms.), is 3 years old. One of a length of 1 ell (c. 60 cms.) weighs 2—3 "mark" (c. 850—1250 gms.), and is 4 years old. One of a length of 5—6 "kvarter" (c. 75—90 cms.) weighs 6 "marker" (c. 2550 gms.), and is 6 years. Pike of the larger kind, with a length of 2 ells (c. 120 cms.) and a weight of 1 1/2 "lispund" (c. 1.3 kgs.) have as a rule 12 or 13 rings upon every vertebra, and ought consequently not be older than 12 or 13 years.¹

An eel weighing 2 "mark" (c. 850 gms.) is 6 years old. Perch of 2 "mark" (c. 850 gms.), 4 years. Codfish of 2 "mark" (c. 850 gms.), 5 years. Bream of 3 "mark" (c. 1250 gms.), 6 or 7 years, etc.

If, as I believe, the growth, at least the growth in length, of the fishes ceases once they have reached a certain age, the number of the rings upon the vertebrae indicates the correct age of the fish only as long as it is still growing. The maximum number of rings found in a fish then indicates the number of years required by this species of fish for reaching mature size. And since presumably fishes, like other animals, can live a long time after they have attained full size, the age of a fish with the maximum number of rings is uncertain. But if, as many believe, at least some type of fish grow as long as they live, then the number of rings would always reveal the correct age. What is the truth in this respect can only be decided by experiences and observations which everybody with an opportunity to do so is invited to make.

¹ This average growth rate no doubt is correct. Editors.

There is, however, no doubt that a knowledge about the age of the fish is of great use economically. For the first it teaches us to spare the young fish. Provided a calf would not be full-grown within 50 or 100 years, what reason could determine me to spare its young life, and not to eat it in its earliest youth? But if I know that in 5 years it will have reached its final size, and then have 15 times the value of its early youth, I am quite willing to spare it in the hope of greater profit and use for myself within a short lapse of time. The same is the case with the fish. As long as one imagines its growth to be so slow, one has not patience to wait for its being full-grown. Therefore it is not spared, but large and small are caught, when and as much as can be obtained, as there are few persons who think of their descendants and for a farther-off future. Of this our forests are deplorable witnesses. But if I know that within a few years, which I myself believe myself able to wait, the fish will attain the size allotted to it by the Creator, I am rather willing to spare it in order to derive from it the greatest profit. What should be the reason for our unreasonable and indefensible way of fishing, when we catch the fish in spawning time and with the mother kill 1000 lives of which every one within some years could be as good as the mother? And that we catch small fry of which 10 hardly suffice to still the hunger of one person, but of which one within some years could sate several? Is it not our ignorance about the age of the fish and its fast growth? I wish to believe that with an increased knowledge about these matters at least some more reflecting husbandmen will be more prepared to spare the young fish until it has reached its full size. To these will belong especially those who are the owners of lakes and thus sole beneficiaries of their good economy. Also all persons who own shares in the same lakes and fishing waters ought to agree on the same economy with the small fish, both for their own and for society's common and great advantage in times to come. If this had been the case in the past, we would not now suffer from such a deficiency of fish, and the lakes which otherwise might be such excellent, rich, and secure storerooms would not be empty.

A second advantage of the above knowledge lies in the encouragement it gives towards the construction of fish-ponds. There should not be many farms in the country, where there is no opportunity for it. But as long as an enterprise does not promise certain and speedy profit, it is usually neglected. In this way the ignorance about the fast growth of the fish is said to be partly responsible for the scarcity of fish-ponds in this country. I would wish that a safer conviction of the speedy profit to be expected from such ponds would encourage our countrymen to pay more attention to such certain, living, and self-replenishing storerooms.

Notes on the Feeding Technique of the Goosander in Streams¹

By ARNE LINDROTH and EVA BERGSTÖM

Introduction

The predation by mergansers on stream fishes has received special attention, since economically important salmon and trout populations are concerned. Investigations in Canada have demonstrated the serious effects of this predation (see WHITE 1957 and for references), and these findings are corroborated for the river Indalsälven in Sweden (LINDROTH 1955, PETERSON 1956) and for some Norwegian streams (AASS 1956). The general behaviour of the mergansers in river Indalsälven was described by HOLMER (1955).

The Swedish investigations revealed that parr of salmon, sea trout and, to a minor extent, bullheads (*Cottus gobio* L.) and, in late summer, grayling fry (*Thymallus thymallus* L.) constituted the bulk of the food in spite of the presence of older grayling and minnow (*Phoxinus aphyu* L.) estimated to be by far more abundant on the feeding grounds than what is expressed by their occurrence in the stomachs. Also other investigators have observed a preference for salmonid fish (SAYLER and LAGLER 1940 for Michigan streams; WHITE 1957 for eastern Canada; AASS 1956 for Norwegian streams). As, in contrast to the other fishes mentioned, the fishes preyed upon live in close contact with the bottom or hide between and under pieces of gravel and stones the assumption was expressed that in streaming water the mergansers adopted some "special feeding technique" — — — "including some kind of working the river bottom in sight of prey or at random" (LINDROTH 1955), and an experimental test of this assumption was pronounced desirable.

This test has now been made.

Experimental

Two clutches of eggs of the goosander (*Mergus m. merganser* L.) were hatched on the 12th and 16th of June 1957, resp., and the ducklings were raised by Mr. J. WIKLUND, an expert breeder of game birds and other animals. On August 14th four ducklings, two from each clutch, were transferred to the stream tank of the Hölle Salmon Laboratory, 10 m long, now set up as a

¹ Report from The Migratory Fish Committee.

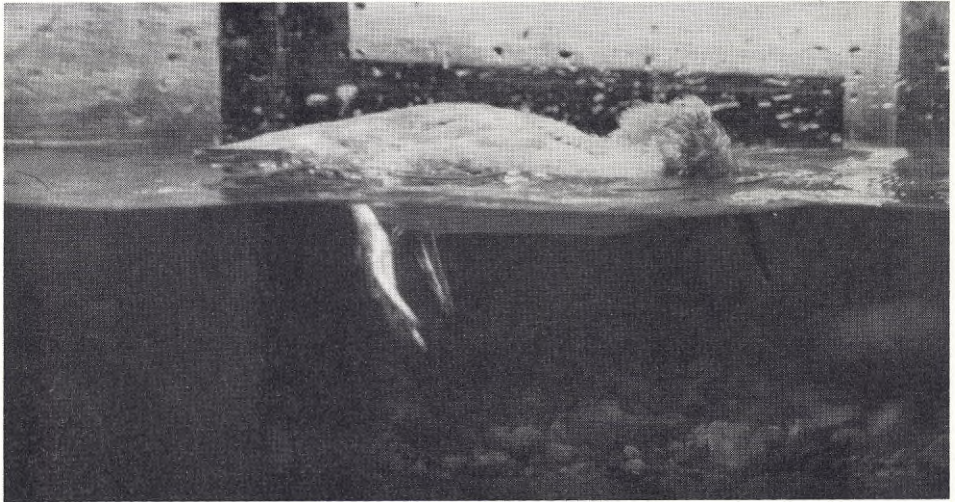


Fig. 1. Young merganser searching the bottom from the surface. — Photo: J. SAHLIN.

stony brook, 80 cm broad and some 60 cm deep. (For details concerning the stream tank see LINDROTH 1954.) The velocity of the water was kept at about 0.5 m/sec.

The birds were observed and photographed through the glass walls of the tank. The experiment was terminated on Oct. 18th.

Observations

On arrival at the laboratory the ducklings were about 9 weeks old. They were not shy, and felt apparently at home already during the first day, swimming, diving, and feeding. A board with an infra-red lamp was put up as resting place, and was used regularly during night. At daytime the ducklings preferred the stones close to the water or the wooden bar separating water and bank halves of the tank. If the light was turned on in the evening the birds almost always went into the water. The light being put out again while they were swimming always put them into great fright, and caused them to rush to the board under the diffuse reddish light, where they struggled for the best place under the lamp. One of the ducklings soon grew ill and weak, and was pushed aside by the others.

During the first time the ducklings remained on the same spot upon the water surface or swam slowly with part of the head, including the eyes, immersed in the search for food (Fig. 1).¹ Air could bubble from the nostrils.

¹ This behaviour has been observed in newly hatched ducklings on their first swim, without mother bird (H. PETERSON personal communication 1958).

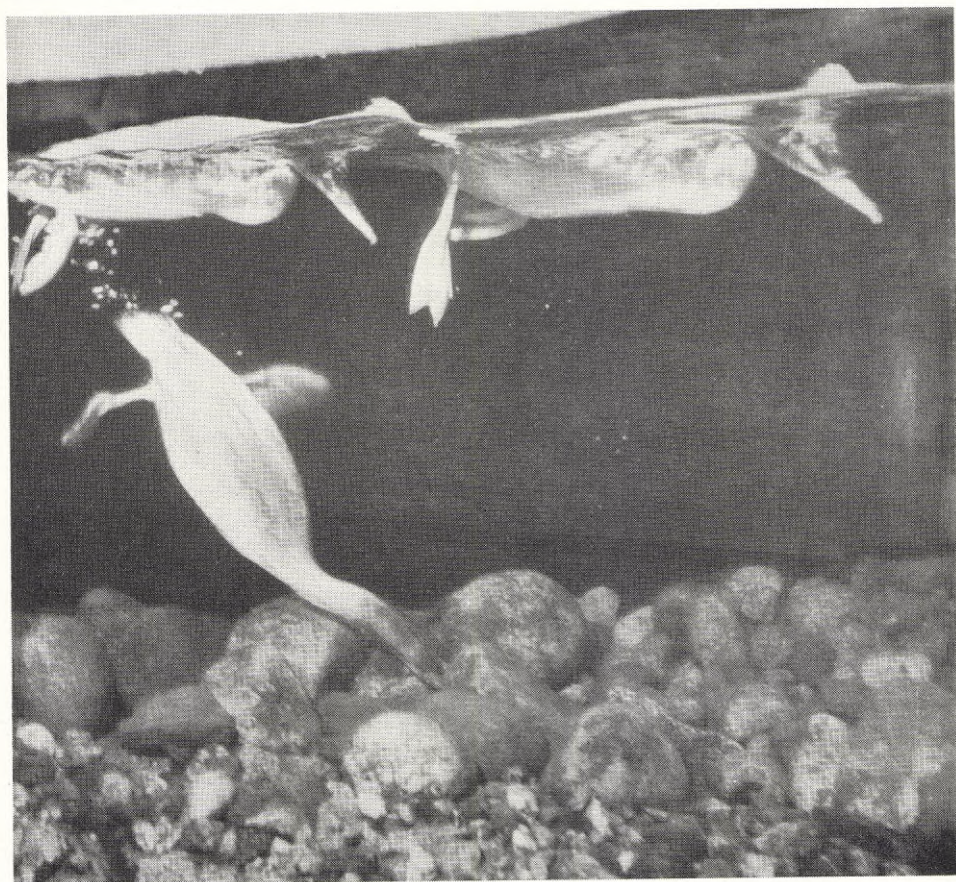


Fig. 2. Alternate leg strokes in the surface, simultaneous strokes when diving. Air leaves the plumage of the diving bird. — Photo. H. PETERSON.

If in this position they caught sight of a fish, they immediately dived without raising the head above the water. One sometimes got the impression that the bird missed the prey for no other reason than for being forced to the surface by want of air. After about a week in the tank the exploring swims on the water surface were faster, and the head was immersed, stretched forward, or moved in jerks. Now they swam also totally immersed in addition to the short divings for seizing a discovered prey. After a month they were expert long-divers.

When swimming on the water surface the mergansers move their legs alternately and in the vertical plane. When diving they change to simultaneous movements. (See Fig. 2.) The plane in which the legs strike varies around the horizontal plane, the return movement being almost vertical (Fig. 3), the back stroke even dorsal to the back (Fig. 4), according to the

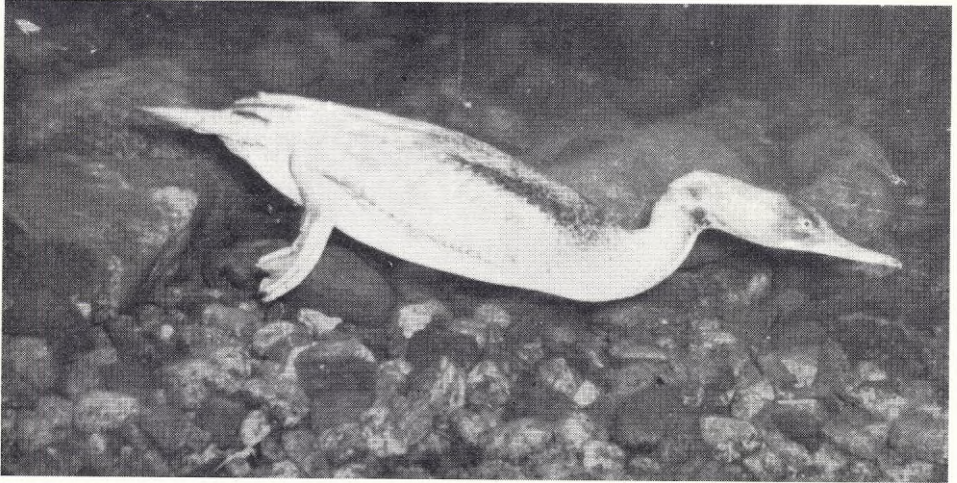


Fig. 3. On quiet long-dive. Tail-rudder steers downwards to give the body an inclination necessary to counteract the updrift. — Photo J. SAHLIN.

needs. The tail-rudder mostly gives the whole flat body the inclination necessary to prevent the duck, moving forward through to the water, from floating to the surface (Fig. 3). The air of the plumage gives the bird a silvery appearance, and leaks out from the rear end (Figs. 2, 4). At the end of an undisturbed dive the leg movements cease, the tail is raised, and the duck ascends passively to the surface (Fig. 5).

A diving merganser moves its head in jerks producing the impression of a walking hen. The back stroke of the leg is accompanied by a stretching of the neck; when the leg is moved forward again the neck is curved to the effect that the forward movement of the body is just neutralized, and the head is kept still in relation to the bottom of the stream for a certain time until, at the next stroke, it takes a new position. An analysis of cinematographic pictures reveals that the rhythmic jerking of the head results in alternating periods of forward movement and of standstill of varying duration which in studied cases of quiet long-dives lasted longer than half the time with fixed head (Fig. 6). When the duck probes the bottom or catches small fish, the jerking becomes irregular. In pursuit of larger escaping prey or when chased the ducks keep the neck more rigid, and the jerks disappear.

From the beginning the birds were quite fearless, and came rushing towards the keeper as soon as they caught sight of him. In case they did not observe him a whistle was enough to start them rushing towards him. Often the food was caught already in the air. As mentioned above one of the ducklings grew weak, and lay most of the day under the infra lamp. In order to assure the feeding of this bird some food was put upon the board. The duckling soon grew accustomed to it, and at feeding time always jumped

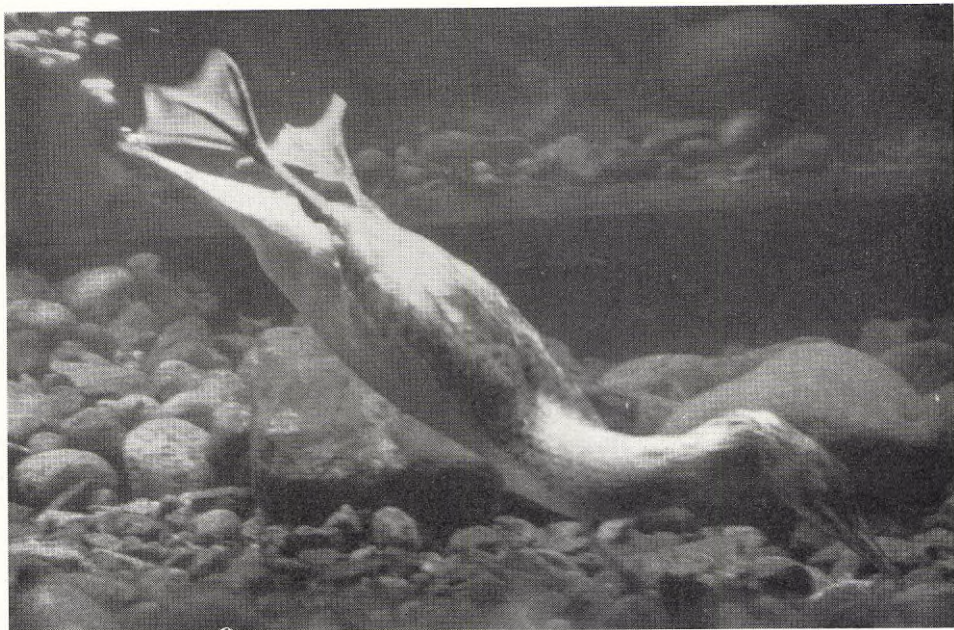


Fig. 4. A forceful stroke behind the back. — Photo J. SAHLIN.

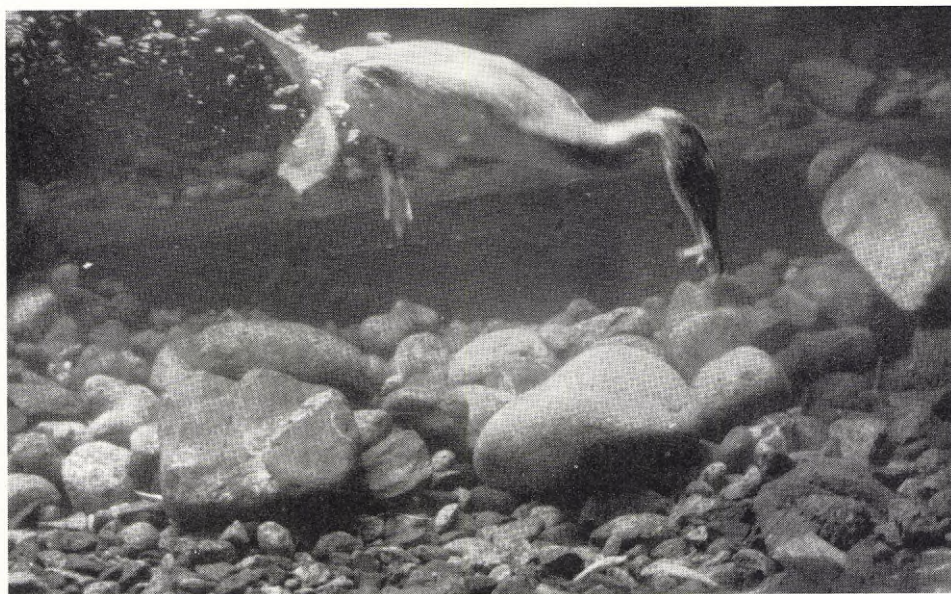


Fig. 5. Floating to the surface, tail bent upwards, with a salmon parr crosswise in the bill.
— Photo: J. SAHLIN.

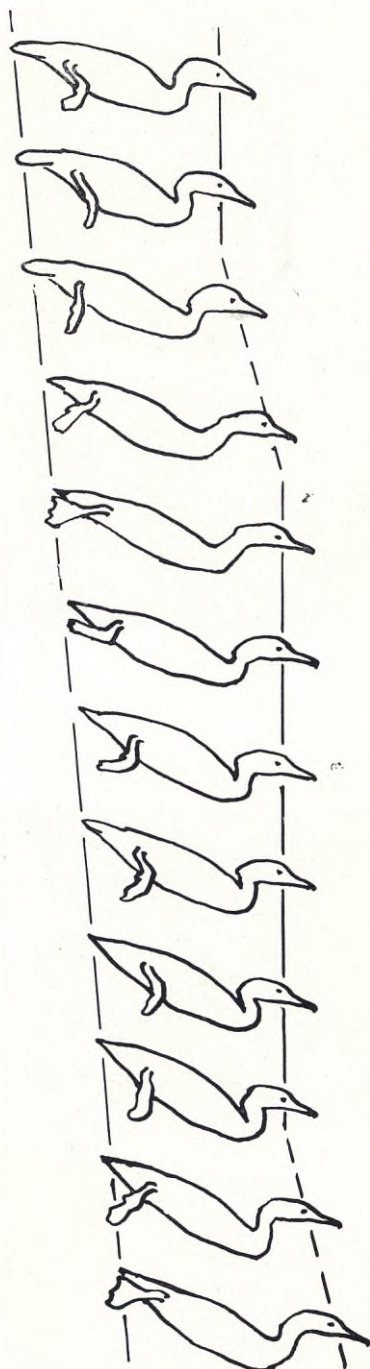


Fig. 6. Twelve successive moments in a quiet long-dive. The full cycle, shown here, the head is stationary for nearly $\frac{3}{4}$ of the time. Film speed 24 per sec. — Photo: H. PETERSON.

upon the board even if it had been swimming before. Soon this habit was adopted also by the others.

The ducklings were mostly given live and dead salmon parr from the rearing station, live roach, and dead Baltic herring. This type of food they preferred to filleted cod which could be left on the bottom of the tank for hours. Sometimes the birds dived repeatedly after pieces of cod only to drop them again. Fish was mostly seized crosswise, but quickly turned, and swallowed head first (Figs. 7—8).

Already on the day of arrival of the birds live fish were put into the tank. This sort of food had never before been presented to the ducklings, but they began immediately an intense chase of the prey. Since then live fish was always chased with great eagerness and tenacity, and as the diving capacity improved the birds could catch and swallow many fishes in succession during one dive. Salmon parr often had no chance of hiding in the bottom before being seized by a bill, and seemed to be easily detected by sight, when moving amongst the stones of the bottom, in fact more easily than a roach swimming in the open water. This indication of a preference for bottom fishes is interesting. It was moreover observed that the birds dived for prey not only, when a fish or other food was actually in sight but also, without this stimulus, for a thorough examination by

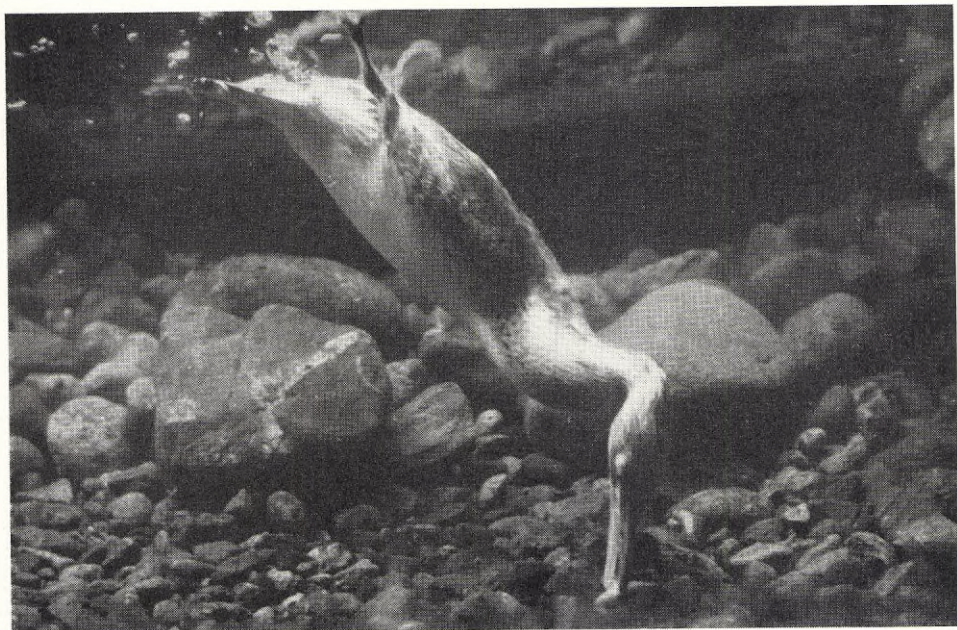


Fig. 7. Just seizing a dead salmon parr. — Photo: J. SAHLIN.

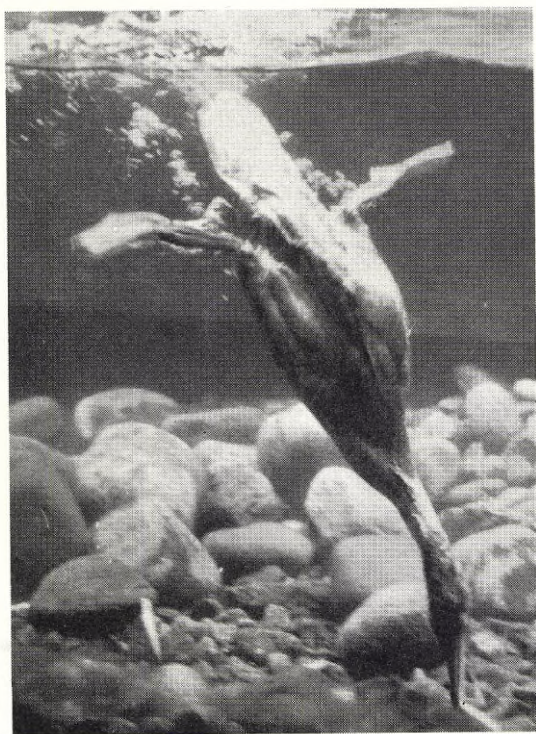


Fig. 8. Directly from the surface. — Photo: J. SAHLIN.

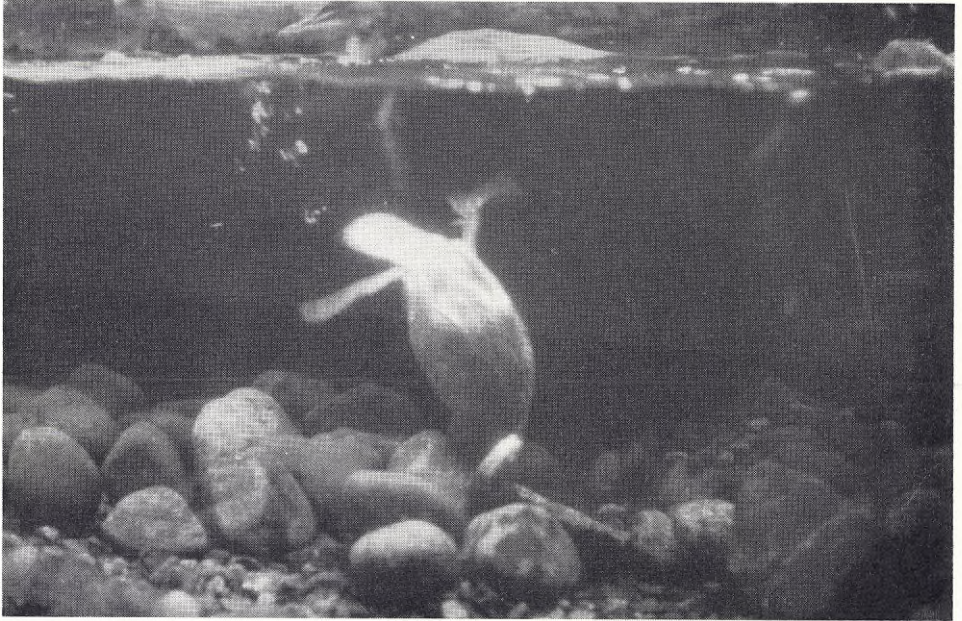


Fig. 9. A diving merganser searching the bottom in the stream tank, for the moment empty of fish. — Photo: J. SAHLIN.

means of the bill of the holes and fissures in the bottom. (Figs. 2 and 9.) Discovered hiding fish were promptly seized and swallowed, either immediately or after a few darts. There was no indication, however, that the birds should try to move pieces of gravel or stones in their search for food.

The least movement upon the bottom was observed by the birds, even mud lumps and the like moving in relation to the bottom.

The ducklings were tagged with red and green rings around one leg. The day after the tagging both red rings and one green, placed on the same leg as one red, were missing. Snapping at one another's feet was observed even when no tags were present. The missing tags were later rediscovered on the bottom. For the red tags the birds dived incessantly, when passing over them, likewise for a glittering piece of glass from a broken bulb. The green tag passed unnoticed.

Discussion

This discussion will be concerned almost exclusively with the fisheries biological aspects of the feeding behaviour of the goosander.

In general our observations agree very well with the statements of WHITE in his recent survey of "Food and natural history of mergansers on salmon waters in the maritime provinces of Canada" (1957). As for the leg move-

ments under water we seem to have observed a more diversified pattern including strokes dorsal to the tail to counteract the updrift force.

The most conspicuous feature of the general behaviour of the merganser is the jerking head of the diving duck. By means of this innate mechanism, established by the cinematographic pictures, the eyes are moved through a series of fixed positions in relation to the bottom the pauses occupying about or more than 50 per cent of the diving time. As pointed out by WALLS (1942) a mechanism of this kind in walking and swimming birds (cf. also the head movements in owls) would furnish "a basis for the estimation of distance and relief". Furthermore, for the discovery of real movements of prey animals it must be of the greatest advantage to avoid the mess of apparent movements in a permanently passing visual field, as is the stream bottom for the mergansers. — In pursuit of a discovered fish, or when chased, the duck permanently fixes its eyes upon the prey or a more distant aim, the need for fixed points of view existing no more, and the jerks disappear.

To the peculiarities of sight in mergansers must be added their accommodation mechanism for underwater vision consisting not only of powerful iridic sphincters which deform the lens but also of "a clear, lens-like central window" in the nictitating membrane (see WALLS 1942).

In agreement with the statement of TOWNSEND (in WITHERBY *et al.* 1945) we never saw the ducks make use of the wings under water.

It is reported that mergansers are "probing with the bill amongst stones to disturb small fish" (MILLAIS acc. to WITHERBY *et al.* 1945), and SALYER and LAGLER (1940) report feeding in shallow streams by probing "under the larger pebbles, rocks, submerged sticks, logs and other cover". Likewise WHITE (1957) assumes that mergansers "will search the shallows and probe beneath stones with their bills", though his references (to WHITE 1939) seems to permit no decision whether the mutilated parr tails result from random probing or from attempts to catch an already perceived fish. It is now beyond doubt that the mergansers search under cover by means of the bill just at random and with no other external stimulus for this appetitive behaviour than a bottom topography with holes and fissures, where parr is likely to occur. In what degree this is learnt by the individual and in what degree the behaviour would be the same on an unfamiliar bottom of the same nature could not be ascertained.

The assumption by SALYER and LAGLER (1940) that "smaller fishes, — — — were presumably swallowed under water" has been verified in this study.

From the first day onwards all observations developed and confirmed a vivid impression of the gruesome effectiveness of the mergansers in cleaning the observation tank from fish, and we are very apt to believe in the sad picture of depleted streams drawn by WHITE (1957), streams, where the

remaining fish "are mostly the very small ones and those which are too large for the ducks to swallow", and where the fish of suitable size are reduced "to the point where the ducks cannot profitably search for them" or left "at places where mergansers are constantly frightened away".

As far as salmon is concerned all fresh water stages, except possibly the very youngest fry and, of course, the spawning fish, are fish of suitable size.

It may be true that predation of a specified predator on a specified prey animal and even predation as a complex unspecified phenomenon is over-estimated as a factor for the control of animal populations (FRASER DARLING 1958). Nevertheless, the Canadian very positive experiences of a considerable increase in smolt output resulting from an active merganser control on the rivers (see e.g. ELSON 1952, WHITE 1957) clearly indicate a role of this specific predator in depressing salmon populations, and our field studies (LINDROTH 1955) and the present tank observations make us believe in this ability of the mergansers to interfere with a salmon parr population, the territorial mosaics of which have been recently clearly depicted by KALLEBERG (1958), to the result that a certain parr population is left the mean abundance level of which characterizes the individual rivers, and is determined by peculiarities of the particular rivers, their bottom topography, extent of human habitation along the riverside, etc.

The river predation, by mergansers and other predators, corresponds to RICKER's predator-prey relationship type C (RICKER 1954), and may be the working agent in a *density-dependent mortality* (*sensu* LACK 1954) or *compensatory mortality* (*sensu* RICKER 1954) or, rather, in maintaining an *absolute survival* level (LINDROTH 1950), by this last term directing our attention towards the main abundance-determining type of factor: in this case the absolute amount of first-class survival-governing territories.

Further discussion of the influence of river predation on salmon stocks will be postponed to a later opportunity.

Thanks are due to Professor F. BERG, Uppsala, for valuable suggestions on visual mechanisms, and to Dr. E. FABRICIUS who kindly looked through the manuscript.

Summary

Ducklings of the goosander without mother bird were observed in a stream tank. As assumed from earlier stomach content analyses the birds practised active search after hiding bottom fishes among pieces of gravel and stones even without the optical stimulus of living or dead food fishes. Whether this is an innate behaviour or learned could not be stated. The role of mergansers in depressing the salmon parr populations towards an absolute survival level is briefly discussed.

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An Electrophoretic Survey of Multiple Haemoglobins in some Fresh-Water Fishes

By GEORG O. SCHUMANN

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1. Introduction

Until recent years the haemoglobin portion of fish blood protein has received very little attention in most serological investigations. The presence of multiple haemoglobin, or haemoglobin having different crystal forms, has been demonstrated for a number of warm-blooded animals. REICHERT and BROWN (1909) found differences in all of the haemoglobins they studied. HEIDELBERGER and LANDSTEINER (1923) in a very interesting study, found that the haemoglobin of the hybrid mule showed similarities to both horse and ass haemoglobin. BOYD (1956) reports that at least ten genetically distinct conditions have been found which may be characterized by differences in the composition of the haemoglobin of erythrocytes, and at least five different kinds of human haemoglobin (Hb) exist.

HASHIMOTO and MATSUURA (1959) report the presence of multiple Hb in several species of salt-water fish, one species of Pacific salmon (*Oncorhynchus keta*), rainbow trout (*Salmo irideus*), and carp (*Cyprinus carpio*). PEDERSON (1933) describes the electrophoretic heterogeneity of a fish (*Opsanus tau*) Hb, and MATSUURA and HASHIMOTO (1957) the electrophoretic separation of tuna (spp.) Hb. MANWELL (1957) found evidence of two Hb fractions in the blood of a salt-water scorpion fish (*Scorpaenichthys marmoratum*) by alkali denaturation.

HASHIMOTO and MATSUURA (1959) first ran a series of electrophoretic Hb separations on five species of fish (Table I) and then demonstrated the presence of multiple Hb by degree of solubility of each fraction in ammonium sulfate, and by measuring the coagulation coefficient of the fractions at

Table I. Electrophoretic analyses of Hb's of fish. For each component, values for the first reading give amount in percent; for the second reading mobility $\times 10^5$ cm.² volt⁻¹ sec.⁻¹

Kind of fish	No. of animals	Component			Buffer
		I	II	III	
Yellowtail <i>Seriola quinqueradiata</i>	1	51 2.0	14 1.2	35 1.0	veronal pH 8.6
Swordfish <i>Makaria mitsukurii</i>	a few ¹	100 1.8	— —	— —	phosphate pH 8.0
Chum salmon <i>Oncorhynchus keta</i>	1	55 2.3	45 1.2	— —	
Rainbow trout <i>Salmo irideus</i>	5 ¹	59 2.6	17 1.8	24 1.6	veronal pH 8.6
Carp <i>Cyprinus carpio</i>	1	73 1.8	24 1.5	— —	
Carp <i>Cyprinus carpio</i> ²	1	100 0.7	— —	— —	phosphate pH 8.0

¹ Combined.

² Met Hb from another individual.

Table abstracted from HASHIMOTO and MATSUURA 1959.

Note. Analyses given were made by Free-Electrophoresis.

various temperatures to derive a heat coagulation curve (for salmon Hb). Column chromatography and spectrophotometric measurements also confirmed the presence of multiple Hb in the blood of the Pacific salmon species investigated.

The writer has investigated the Hb of a series of fresh-water fish by means of Agar-electrophoresis and has found, as supposed by HASHIMOTO and MATSUURA (op. cit.), that heterogeneity of blood Hb is widespread in fishes. This work was undertaken in an effort to separate, serologically, the sibling species reported by SVÄRDSON (1957) and to determine if there are serological differences between the large and small char forms, *Salmo* (*Salvelinus*) *alpinus*, which inhabit some lakes in northern Sweden.

2. Materials and Methods

The analyses of fish Hb was made in an agar-agar medium with a modified electrophoresis apparatus suggested by KUNKEL and TISELIUS (1951). Concentration of agar in the medium was 5 g in 500 ml buffer. Borate buffer was used in which 6.422 g H₃BO₃ was dissolved in 1 liter 0.1 N NaOH: the final solution adjusted to pH 8.6. Borate buffer was found, on comparison, to give as satisfactory results as the more expensive veronal acetate buffers. The source of power was usually 220 line voltage stepped up to 250 volts by transformer and converted to direct current by means of a selenium rectifier. This gave from 3 to 4 milliamperes depending upon

the power supply. It was necessary to transport the apparatus to various places when investigating the Hb of fish found only in restricted areas, and at many times the power source was not of the same voltage.

The procedure in preparing the agar slide was to pour 40 ml. of buffer containing 0.4 g of agar in solution into a rectangular plastic tray having removable ends. This gave a bottom layer of circa 1 mm. in thickness. After the agar had cooled, six glass strips 0.7×2.0 mm. cut from 1 mm. thick window glass were placed upright on the agar at intervals across the center of the tray, and a second layer of 40 ml. solution was poured. Shallow pits were formed in the upper 1 mm. layer when the glass strips were removed. The tray containing the agar slide had a built-in chamber where cooling water was circulated, but since the cooling effect depended upon the tap water temperature at the time of the experiment, the temperature of the slide varied.

After electrophoresis had produced a maximum separation in the sample, the agar strip was slid off the carrying tray into a dish of 10 % acetic acid to fix the proteins, thus preventing the fractions from migrating radially from the point of concentration. The strip was then transferred to a solution of Amino-black stain, where it remained from one to two hours. Destaining was accomplished by washing in cold, running water until the agar surrounding the stained portion became clear.

Blood was collected from fish by two methods. When working with large fish, the distal portion of the Bulbus arteriosus was severed and blood allowed to run into a test tube containing cold physiological saline and sodium citrate. The tube was tipped back and forth to mix the contents and immediately placed in a beaker of ice (when available). Small fish were very difficult to work with and not much success was had using the methods commonly employed to obtain blood from larger fish, i.e. severing the tail etc. It was found that after cutting across the bulbus, small fish could be dropped into an iced beaker saline containing citrate and allowed to swim about. The slime and other contaminants found in the resulting diluted blood solution could be removed by repeated washing with cold saline. Adequate samples of erythrocytes were thus obtained from such small species as *Cottus* and *Phoxinus*. All samples of erythrocytes were washed and centrifuged three times before being haemolyzed with distilled water.

An effort was made to treat all samples uniformly when it was possible to do so. At various times it was necessary to walk some kilometers to lakes containing a certain species. In this case, blood was taken from the fish immediately before returning and was transported in cooled containers. In most instances blood was centrifuged a few minutes after being collected and the serum pipeted off. After being washed, 0.1 ml. of the centrifuged cell suspension was hemolyzed in one ml. distilled water and the resulting hemolysate centrifuged again to settle the cell debris. The clear hemolysate was then analysed as soon as possible.

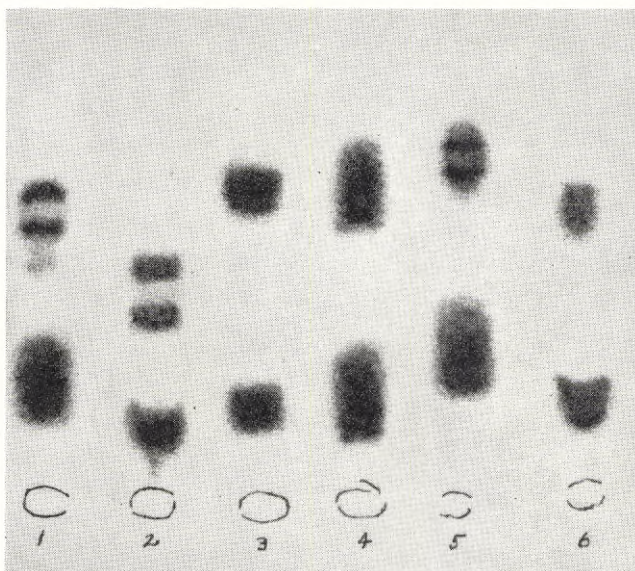


Fig. 1. The electrophoretic pattern of fresh Hb from six species of fish. 1. *Salmo alpinus*, 2. *Salmo t. lacustris*, 3. *Salmo t. trutta*, 4. *Salmo salar*, 5. *Thymallus thymallus*, 6. *Cottus poecilopus*.

3. Discussion of Methods

After the investigation was begun it was found that the results obtained in electrophoresis were many times influenced by the condition or treatment given samples. HASHIMOTO and MATSUURA (1959) report on the number of Hb fractions obtained electrophoretically from the Hb of dead fish (two species of salt-water fish) which had been stored in ice for some time. The present investigation indicates that there is a deterioration of some of the faster migrating fractions (the smaller Hb molecules) with the death of the fish and it was not possible to obtain the same degree of separation of fractions in old samples as was possible with fresh material. In every instance, however, no additional fraction was obtained from stored material or Hb obtained from blood of dead fish. In most instances there was a "loss" of one or more fractions. That is, one or more fractions would not migrate with critical boundaries, but would blur into each other so it was impossible to determine if one, or more than one fraction was present in a migrating band. Figure 1. illustrates the electrophoretic pattern of fresh Hb from six species of fresh-water fish. The faster components are very nicely separated with sharp boundaries. Figure 2. illustrates an agar slide containing the pattern formed from the same samples of Hb as were used in figure 1, but in this instance the Hb had been stored for several weeks.

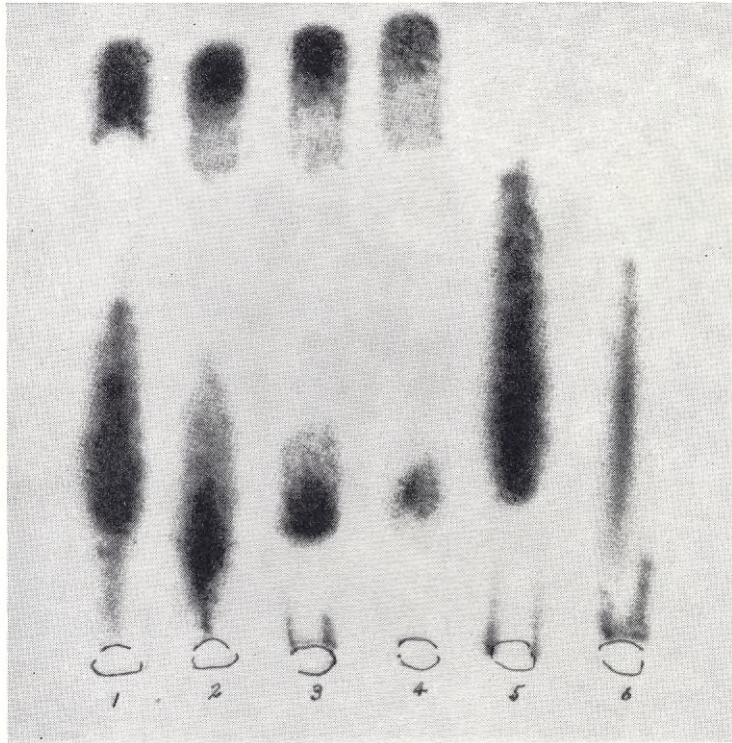


Fig. 2. The electrophoretic pattern of Hb from stored samples (used in Fig. 1) 1. *Salmo alpinus*, 2. *Salmo salar*, 3 *Salmo t. lacustris*, 4. *Salmo t. trutta*, 5. *Thymallus thymallus*, 6. *Cottus poecilopus*

HASHIMOTO and MATSUURA (1959) mention that there was no deterioration of their samples when stored at -20°C . The writer has not had occasion to store many samples, and none were stored at this low temperature, but there is evidence that the degree of deterioration depends to some extent upon the species concerned. This is due to the circumstance that in a species such as *Abramis brama*, which has two (see following pages) widely separated Hb fractions in electrophoresis, any alteration of the faster fraction would not be very apparent. In the *Coregonus* species tested, three fractions are present. The two fractions which migrate faster than the third fraction have very critical boundaries, and any alteration in the fractions would cause them to migrate as one band (see Fig. 2).

To date it has not been shown what the optimum pH of the buffer should be to obtain the best possible separation of Hb fractions. There is some indication that each species will have differing requirements for optimum Hb separation. Figure 3 illustrates migration at various pH values. In this instance, however, the lower pH values were obtained by additional amounts

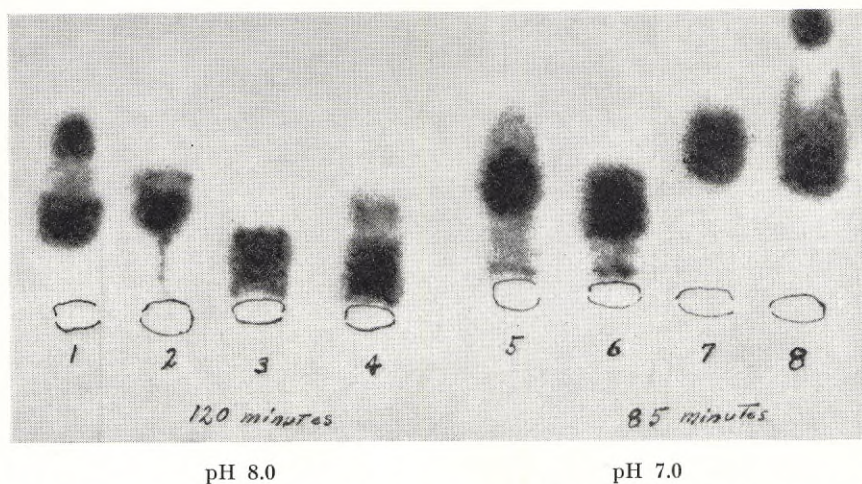


Fig. 3 a. Migration of Hb at various pH values. 1. *Abramis brama*, 2. *Leuciscus rutilus*, 3. *Perca fluviatilis*, 4. *Esox lucius*, 5. *Esox lucius*, 6. *Perca fluviatilis*, 7. *Leuciscus rutilus*, 8. *Abramis brama*.

of H_3BO_3 in the solution and there was also a distinct temperature variance between the tests which was caused by increased electrical conductivity of the buffer.

Whole fish blood has been found by the writer to be in pH range 6.9 to 7.1 depending upon the species. Upon standing for some minutes, the whole blood of *Esox lucius* changed pH to a somewhat higher value (7.0 to 7.5 after 10 minutes). A determination of the pH of the various species has not been

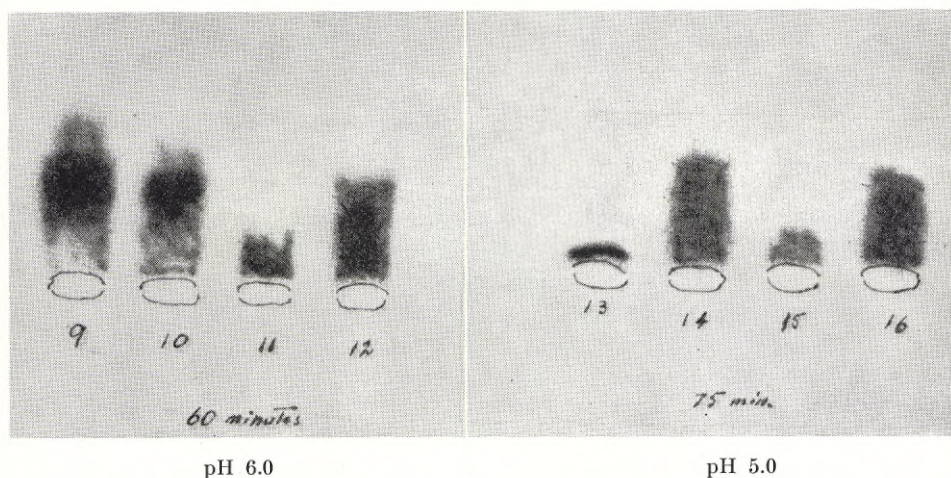
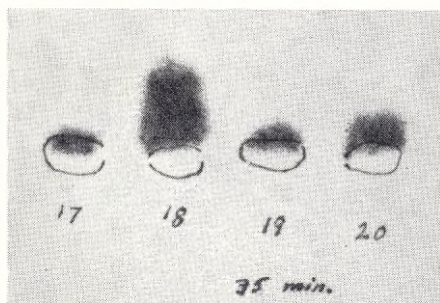


Fig. 3 b. 9. *Abramis brama*, 10. *Leuciscus rutilus*, 11. *Perca fluviatilis*, 12. *Esox lucius*, 13. *Lucioperca sandra*, 14. *Esox lucius*, 15. *Perca fluviatilis*, 16. *Abramis brama*.



pH 4.0

Fig. 3 c. 17. *Lucioperca sandra*, 18. *Esox lucius*, 19. *Perca fluviatilis*, 20. *Leuciscus erythrophthalmus*.

attempted by the writer, nor has a determination of the isoelectric points been made. Blood proteins have molecular electrical charges and the magnitude of these charges vary depending on the protein and the distance of the pH value of the buffer from the isoelectric point, i.e. the point where the electrical charge of the protein molecule corresponds to the field strength of the medium (in this case the agar slide).

The results obtained in Figure 3 may therefore indicate that some species have differing isoelectric points. It may be seen that as the pH value lowers, the migration of the Hb is materially effected; *Esox lucius* being less effected than *Perca fluviatilis*. LUNDGREN and WARD (1951) report that migration of antibodies isolated from a number of animal serums vary in direction and speed depending upon pH of the solution, and that the serums had isoelectric points varying from 4.4 to 5.8. At low pH (3.1) some serums migrated to the plus pole and at higher pH to the negative pole during electrophoresis.

Rate or speed of migration seems also to be somewhat influenced by the concentration of Hb in the sample and this in turn influences the degree of separation obtained in a given distance. Thus samples containing "optimum" amounts of Hb will migrate at different rates than samples containing higher or lower concentrations as may be seen in Figure 4. From right to left, the pits were charged with "full strength" Hb, Hb diluted one-half and to one-fourth of the concentration in the original sample. Figure 5 illustrates the effects of Hb concentration from "full strength" to very low concentrations in the migration of *Coregonus albula* Hb. In lower concentrations, the faster migrating components, present in very small amounts, do not represent a very distinctive pattern. It will be noted, however, that the components shown in Figure 5 have all migrated at about the same speed and there is not the extreme variation as seen in Figure 4. This is because the original concentration of Hb in the sample from *Coregonus albula* was low.

This species, among others, dies very quickly when caught in gill nets and it was difficult to obtain adequate numbers of fish when the experiment

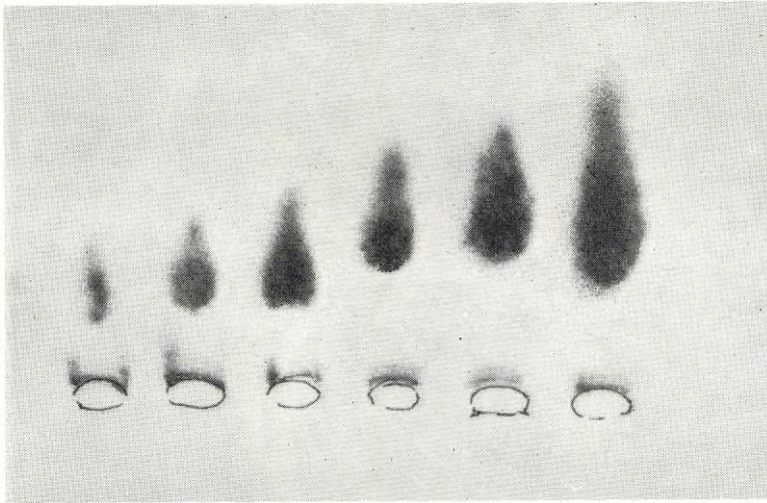


Fig. 4. The effect of concentration on migration of Hb. The three pits to the right contain *Lucioperca sandra* Hb, to the left *Esox lucius* Hb in varying amounts.

was made. The Hb of this species apparently degrades very soon when the fish is held motionless by the net. The Hb of very sensitive species may also undergo a change from the oxyhaemoglobin to the methaemoglobin form of the haemoglobin molecule while the fish is still alive. Presumably oxygen deficiency or other physiological factors could cause this to happen. In most instances, Oxy Hb does not change to Met Hb until after the material has stood for a time; warming hastens this change also. In the Met form the

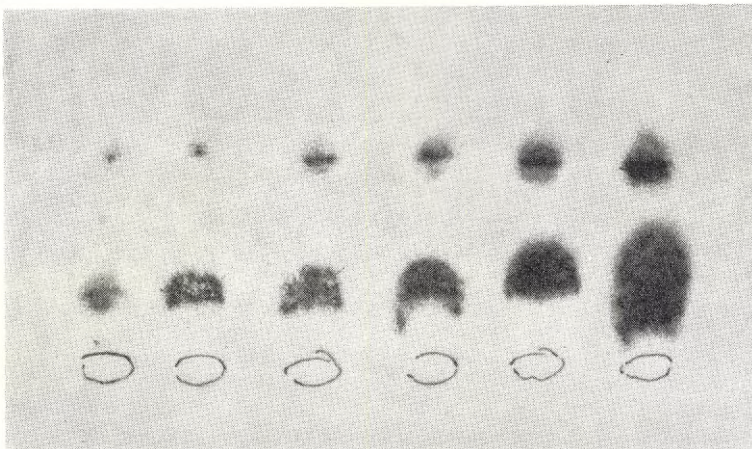


Fig. 5. The effects of very high dilution on migration of Hb of *Coregonus albula*. Each pit, from right to left, received one-half the amount of Hb placed in the preceding pit.

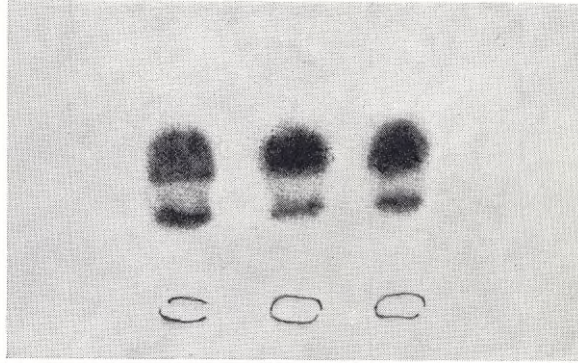


Fig. 6. Hb of *Lota lota*. The I fraction is followed by a small amount of I- fraction. (Time of migration 480 Min.)

oxygen is more closely bound to the molecule, but just how this effects mobility is not clear.

The condition of the fish (other than oxygen deficiency) prior to the blood samples being taken might also have some bearing on the number of Hb fractions which will show up in electrophoresis. Starvation seems to have little effect in this connection, since a comparison of Hb from freshly caught fish and fish held without food for several weeks indicates little change in the Hb takes place. HASHIMOTO and MATSUURA (1959) report that regardless of the individual or sex, the components of salmon (*Oncorhynchus keta*) Hb were found to be present in almost constant ratio. The present work is in complete agreement with these findings, in that all fish examined maintained characteristic species patterns and percentage ratios when adequate and equal samples were compared.

All of these factors suggest that the number of Hb fractions reported for fish species to date, and including the present paper, are minimum numbers and it is very likely that some species have a higher number of Hb fractions.

4. Terminology of Hb Fractions

As far as is known to the writer, Hb fractions have only been termed I, II, III, or F for "fast" component and S for "slow" component, as used by HASHIMOTO and MATSUURA. In most of the fish tested by the writer, Hb seems to migrate as a large, slow moving fraction with perhaps one or more faster migrating fractions which vary in percent of total Hb in the sample. This seems to occur in the majority of cases when fish have at least two Hb fractions. In one species (Fig. 6) the large fraction although moving very slowly, has a small trailing fraction which migrates even slower. So far, *Lota lota* is the only species in which this has been observed to occur. It is



Fig. 7. The differential migration of six species of fish. 1. *Lucioperca sandra*, 2. *Leuciscus erythrophthalmus*, 3. *L. rutilus*, 4. *Salmo fontinalis*, 5. *Perca fluviatilis*, 6. *Abramis brama*. Duration of electrophoresis 420 minutes.

proposed, therefore, to term the large, slow moving fraction "I" and a smaller, but slower migrating fraction as "I-". Thus I will refer to the large fraction which is nearest the starting point, and II or III refer to fractions which migrate at somewhat higher velocities.

5. Results and Discussion

After the Hb of a number of species had been investigated it became evident that the Hb of each species migrated at a definite velocity, other factors being equal. Figure 7 illustrates the differential migration of six species of fish. Figure 8 duplicates the same experiment with some of the species replaced with others. It may be seen that perch (*Perca fluviatilis*) shows only one Hb fraction to be present in its blood (see following pages) and this fraction tends to migrate at the same relative speed in both figures.

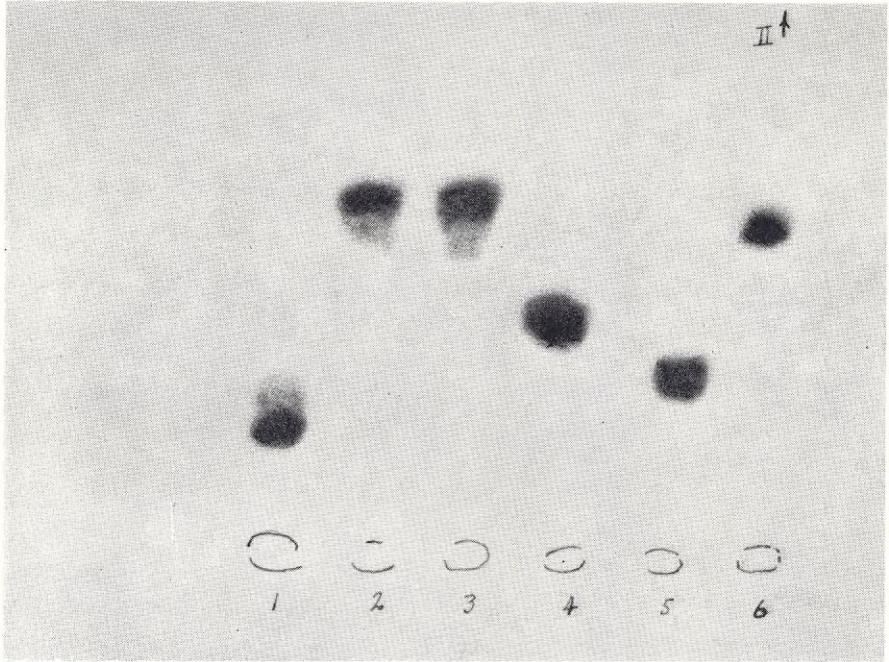


Fig. 8. The differential migration of six species of fish Hb. The relative positions of numbers 2, 3, 5, 6, remain the same as in Fig. 7. 1. *Esox lucius*, 2. *Leuciscus erythroptthalmus*, 3. *L. rutilus*, 4. *Tinca tinca*, 5. *Perca fluviatilis*, 6. *Abramis brama*. Duration of electrophoresis 420 minutes.

In order to determine the difference, if any, in the migration of Hb from different individuals, the Hb of six specimens of the same species was tested. Figure 9 shows that there is very little apparent difference in the rate of migration between individuals. In this instance, the quantity of Hb in each sample was controlled by comparing each sample to a color standard, and diluting the sample until visual uniformity of samples was obtained.

Species showing homogeneous Hb

To date, five species of fish seem to have homogeneous Hb. It must be emphasized, however, that there could be two or more Hb fractions present which migrate at much the same speed and therefore would seem to migrate as one homogeneous band. The closely related species *Leuciscus rutilus* and *Leuciscus erythroptthalmus* are interesting in that the one fraction present in the Hb migrates with exactly the same velocity (Fig. 10). A number of tests made with Hb of these two species show complete uniformity in all cases. *Perca fluviatilis* and *Tinca tinca* (Fig. 7—8) also show only one apparent Hb fraction in a series of tests involving a number of specimens.

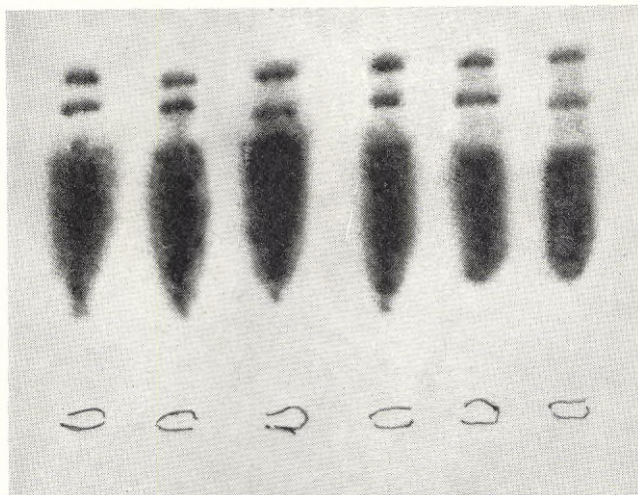


Fig. 9. The migration of Hb from six different individuals of *Coregonus nasus*. Each sample was of uniform Hb concentration.

Because only one specimen of the goldfish (*Cyprinus auratus*) was tested (Fig. 11), the finding of a single Hb fraction is not thought to be conclusive. HASHIMOTO and MATSUURA (1959) report finding two Hb fractions in one carp (*Cyprinus carpio*) and only one fraction in a sample from another fish (Table I). In this instance, the test having only one Hb fraction was made with Met-Hb.

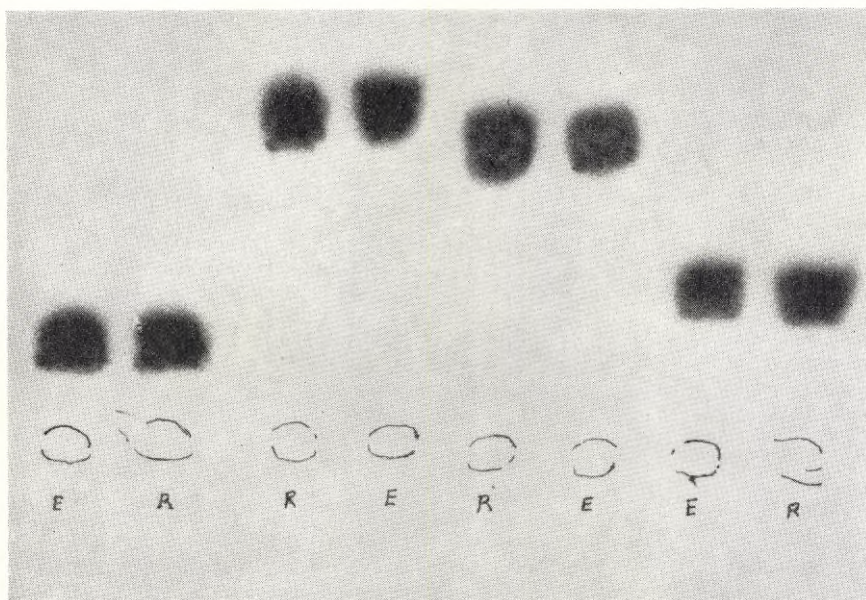


Fig. 10. Four tests which show the uniformity of migration in *Leuciscus erythrothalmus* (E) Hb, and *Leuciscus rutilus* (R) Hb.

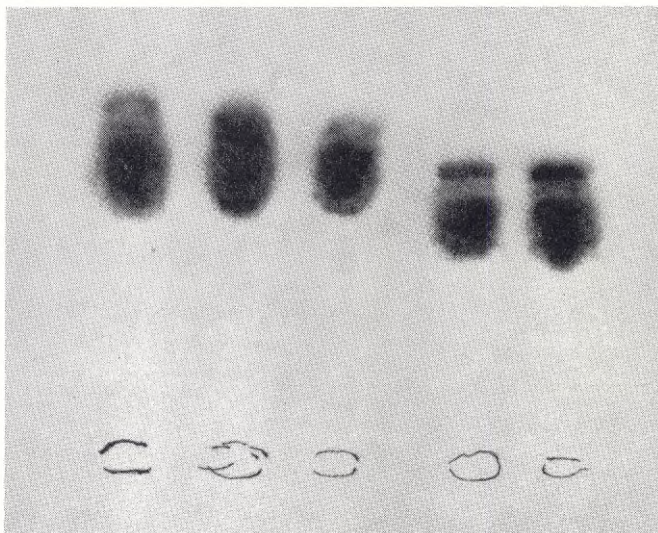


Fig. 11. Hb patterns of two Cyprinid fishes, *Cyprinus carassius*, to the right of the Figure, has two Hb fractions. *Cyprinus auratus*, to the left, does not show indications of having more than one Hb. Duration of electrophoresis; *C. auratus* 7 hours, *C. carassius* 8 hours.

Species showing dual Hb

Very likely the cyprinid fishes have at least two Hb fractions; the results obtained with *Cyprinus auratus* and the carp which showed homogeneous Hb notwithstanding. The closely related cyprinid, *Cyprinus carassius* (Fig. 11), has in all tests to date shown the presence of two components which migrate at almost equal velocities. Fraction II requires a long time (7—8 hours) to migrate through fraction I to become apparent as a less dense leading element. The limitations of the apparatus prevented unusually long runs which might have resulted in a complete separation of the fractions.

A group of 13 species have been found to exhibit evidence of at least two distinct Hb fractions (Fig. 12). The two *Abramis* species are of particular interest. *Abramis brama* and *Abramis blicca* have two Hb fractions each, but the II fraction of *Abramis blicca* migrates twice as fast as the II fraction of *Abramis brama*. The I fraction of both species migrates at the same speed and seems to be of approximately the same percentage of the total Hb in the sample. Species differentiation can always be made when the Hb of the two species are placed side by side in the same electrophoresis run.

The reason for the differential migration of the II elements in these very closely related species (natural hybridization seems to occur frequently in some lakes) is not apparent at this time. If the difference should be due to the II fractions having differing isoelectric points, however, then there is a very great possibility that all closely related species (*Leuciscus rutilus* and

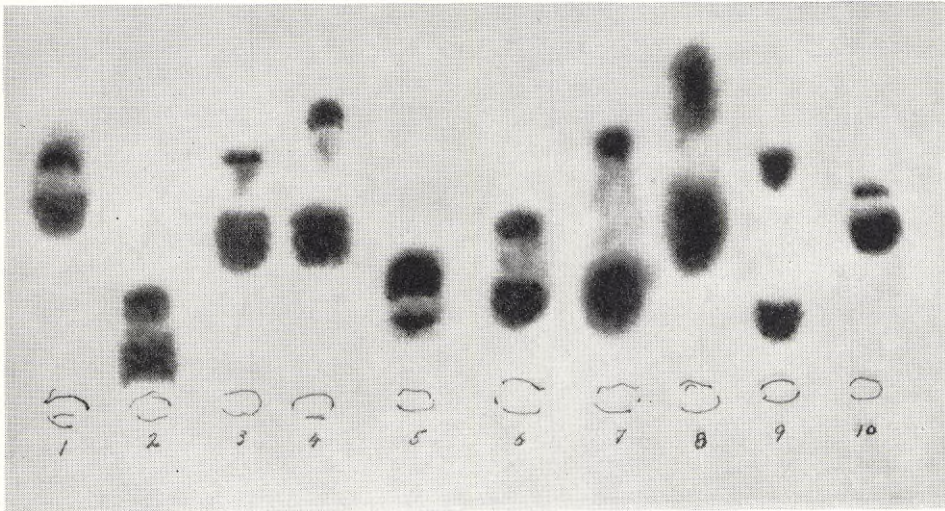


Fig. 12. Hb patterns of nine species of fish having two fractions. Time required for migration as shown follows species name. 1. *Cyprinus carassius* 8 hours, 2. *Lucioperca sandra* 4 hours, 3. *Abramis brama* 8 hours, 4. *Abramis blicca* 8 hours, 5. *Lota lota* 7 hours, 6. *Lucioperca sandra* 8 hours, 7. *Esox lucius* 8 hours, 8. *Acerina cernua* 10 hours, 9. *Cottus poecilopus* 5 hours, 10. *Phoxinus phoxinus* 8 hours.

L. erythrophthalmus for instance) having almost identical Hb characteristics can be differentiated by pH manipulation. If the pH of the medium should be adjusted close to the isoelectric point of one species, the Hb of the related species may continue to migrate, thus indicating some degree of species or race distinction.

Lota lota Hb has a pattern upon electrophoresis that seems to be confined to this species alone; at least it has not been observed in any other species studied to date. The I fraction of most species contains the largest percentage of the Hb found in the sample; this is nearly always the slowest moving fraction. In *Lota lota* Hb, the I fraction is trailed by a I⁻ fraction which contains only a small portion of the total Hb in the sample. (Fig. 12). This trailing I⁻ fraction is thought not to be just an artifact which happens to be left in the medium after the main body of Hb has passed through. This has never happened with Hb of other species, but always occurs when *Lota lota* Hb is electrophorized.

The Hb of *Lucioperca sandra* and *Esox lucius* (Fig. 12) was tested a number of times before a satisfactory separation was obtained. The Hb of these species has been found to be extremely sensitive to aging and must be subjected to electrophoresis soon after it is obtained from the living fish. The agar medium must also be maintained at a low temperature while the run is in progress. In a number of instances, Hb samples from these species

were not held ice cold while they were being washed and centrifuged, and consequently the II fraction, which migrates only slightly faster than the I fraction, did not separate discernably. It seems likely that Oxy-Hb of these species changes very quickly to the Met form upon warming. Specimens tested later in the spring did not seem to have this tendency, probably because the lake water (and fish body temperature) was considerably warmer.

Acerina cernua, *Phoxinus phoxinus* and *Cottus poecilopus* are small species, thus a number of each species had to be combined in order to obtain adequate quantities of erythrocytes for analysis. Presumably the method of obtaining blood, i.e. letting the fish swim about in citrated saline while they bled, resulted in all Oxy-Hb changing to Met-Hb. In every instance a number of tests (with the same samples) gave uniform results (Fig. 12) and the three species showed differing, but consistent Hb patterns. In *Cottus poecilopus* and *Acerina cernua* Hb, the II fraction migrates from two to three times faster than the I fraction. *Phoxinus phoxinus* Hb seems to be characterized by a very small II fraction which migrates only slightly faster than the I fraction.

Two or possibly three salmonid fishes have been tested which show only two Hb fractions in their blood. This is surprising because the majority of the salmonids investigated show at least three distinct Hb fractions upon electrophoresis. HASHIMOTO and MATSUURA (1959) report that they obtained only two distinct fractions upon electrophoresis (Starch and free-electrophoresis, and other methods) of Hb from a species of Pacific salmon (*Oncorhynchus keta*). The writer would have suspected his own results if it were not for the confirmation that some salmonids have only two Hb fractions. The various analytical methods of the above named authors, in checking the results of their own electrophoresis findings, make the presence of dual Hb in some salmonids indisputable. The I fraction of *Oncorhynchus keta* is reported to contain 55 %, and the II fraction 45 % of the total Hb in the sample (see table I.).

The Atlantic salmon (*Salmo salar*) investigated by the author also seems to have only two components (Figures 1—13) and the percentages of Hb in each fraction are in close agreement with corresponding percentages given for the Pacific species named. The Atlantic salmon studied had been living in a hatchery for 10 years since the fry stage. Sea-run brown trout (*Salmo trutta trutta*) and the landlocked form (*Salmo trutta lacustris*), of the same age as the salmon, were also present in the hatchery. These fish had been reared in the same water, received the same food and had an environment in common which was the same in every conceivable way. A most surprising development occurred when the Hb of the three species (forms) was investigated (Fig. 13). The Hb of *Salmo salar* and *Salmo trutta trutta* consistently showed only two distinct fractions, while *Salmo trutta lacustris* always produced three distinct Hb fractions. The II and III fractions migrated very close

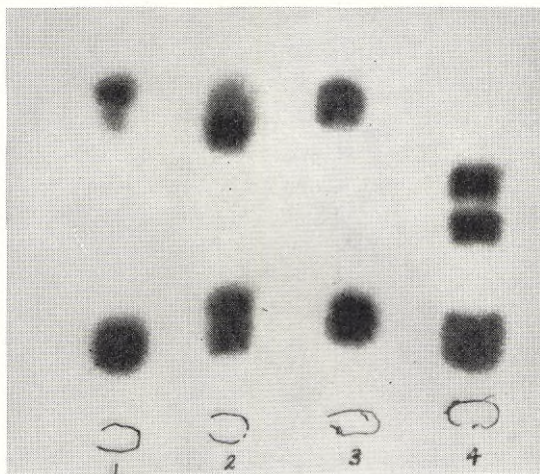


Fig. 13. Hb patterns of 1. *Salmo trutta fario*, 2. *Salmo salar*, 3. *Salmo trutta trutta*, 4. *Salmo trutta lacustris*. Duration of electrophoresis in 1, 2, 3, was 8 hours; number 4 was 3 hours.

together, but separated from the I fraction very soon after electrophoresis had begun. This seems to be usual in other salmonid species studied (possible exceptions being *Coregonus albula* and *Thymallus thymallus*). *Salmo trutta trutta* II fraction also migrates at a relatively faster rate than the III fraction of *Salmo trutta lacustris*.

When the differences between the two forms of brown trout were seen, it was of some interest to learn if Hb of the brook form (*Salmo trutta fario*) would migrate as two or three fractions. Subsequently two small specimens were obtained from Semlanån, a small stream which supposedly contained *S. trutta fario*, and the combined blood subjected to electrophoresis. The Hb of these fish migrated as two fractions much resembling those of *S. trutta trutta*. It must be noted, however, that there is a hatchery near the stream and it is not certain under the circumstances if the specimens tested were "genuine" *S. trutta fario*, or were in reality small *S. trutta trutta* which had escaped from the hatchery. The hatchery manager asserted that fish from the hatchery had not been stocked in the stream, but since the factor of fry escaping is a possibility, the data on *S. trutta fario* must be considered inconclusive until fish of known origin are examined.

The sea-run and landlocked forms of the brown trout studied, were offspring of fish of known parentage, thus the difference in both number of fractions and the speed of migration of fractions points up some interesting theories. There has been a difference of opinion, dating back many years, as to whether the fish are separate species or merely the same species having forms which may or may not migrate to sea.

SCHNAKENBECK (1940) investigated the juvenile development of the three *Salmo trutta* forms (among other species) and is of the opinion that there are discrete, but definite differences present. He considers *S. trutta trutta* and *S. trutta fario* to be more similar in juvenile development than they are to *S. trutta lacustris*, but that all three species have progressed quite some distance along the path of divergent evolution. OTTERSTRÖM (1936), on the other hand, is of the opinion that the forms are not yet completely separated, but that *S. trutta trutta* and *S. trutta fario* are also more closely related to each other than they are to the landlocked form *S. trutta lacustris*. ALM (1948) and FABRICIUS (1953) are of the opinion that there exists no principal inherited difference between the forms, and that differences are the result of environment (ALM) or food supply (Fabricius).

It is noteworthy, in this connection, that in North America where the brown trout (*Salmo trutta fario*) has been introduced, the form does not grow very large; 3—5 kilo being a very large fish. Many rivers and small streams flowing into the Great Lakes and other large bodies of water contain populations of *S. t. fario*, but no population of very large, lake dwelling brown trout similar to *S. t. lacustris* has developed. In large Swedish lakes *S. t. lacustris* reaches a considerable size and weight; specimens of 5 kilo being relatively common and fish up to 15—16 kilo are not infrequently encountered here and in other areas of Europe where large lakes are found.

Whether *S. salar*, *S. trutta trutta* and *S. trutta fario* have a third Hb fraction which migrates at much the same velocity as the II fraction, and thus is not readily evident, must be determined by future studies on the three species. It would seem highly probable that a third fraction is present (at least in the *S. trutta* forms) in light of the results obtained with Hb of the other members of this family.

Species with multiple Hb

Of the species of fresh-water fish studied to date, only the salmonidae exhibit more than two distinct Hb fractions in electrophoresis. Seven species of salmonid fishes have been found to have heterogeneous Hb which contains three distinct fractions. HASHIMOTO and MATSUURA (1959) report that an eighth species, the rainbow trout (*Salmo irideus*) (See table I) has three Hb fractions also; the II and III fractions migrating comparable to the corresponding fractions of the species studied by the present writer. Unfortunately, the Hb of the species shown in Figures 13—14 were not electrophorized under exactly the same conditions and therefore the results cannot be accurately compared in regard to absolute rates of migration.

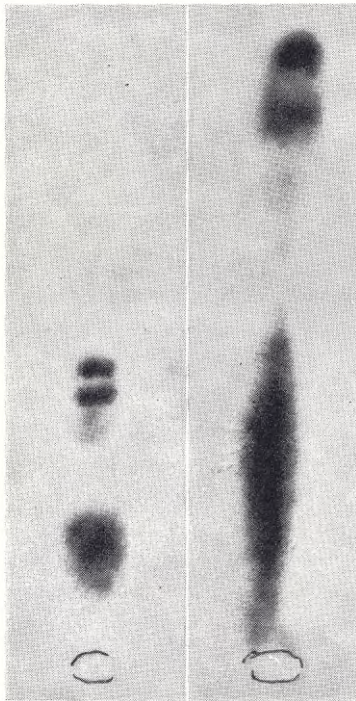
In almost all instances, the II fraction quickly separated from the I fraction, and after a short time the III fraction migrated through the II fraction, to become a distinct band. It is noteworthy that the Hb fractions of the North American char *Salmo (Salvelinus) fontinalis* and the Swedish specimens of



Fig. 14. Hb patterns of five species showing multiple Hb fractions; duration of electrophoresis follows species name. 1. *Salmo (Salvelinus) fontinalis* 8 hours, 2. *Salmo (Salvelinus) alpinus* 7 hours. 3. *Coregonus nasus* 4 hours, 4. *Coregonus oxyrhynchus* 4 hours, 5. *Coregonus albula* 10 hours.

Salmo (Salvelinus) alpinus migrate at approximately the same speed, but the separation of the III fraction takes a longer time in *S. fontinalis* (Fig. 14). A comparison of the Hb of northern *S. alpinus* with Hb of a large char form (sometimes named *S. salvelinus salvelinus*) from Lake Vättern in southern Sweden, show some differences. Due to circumstances, it was impossible to obtain fresh material from both forms at the same time and thus test the Hb simultaneously. The stored Hb from Vättern char had been frozen for several months and undoubtedly changed from Oxy-Hb to Met-Hb. A comparison of *S. alpinus* Oxy and Met-Hb (same sample stored some days in refrigerator) (Fig. 15) shows that although all fractions are present in the Met sample, the time of separation and other characteristics have materially altered. The II and III fractions of Met-Hb did not separate until the sample had been undergoing electrophoresis for 12 hours and had migrated some five cm. from the starting point. The two leading fractions also never became very distinct bands, but showed two areas of higher concentration in the same band.

A comparison of Met-Hb from northern and Vättern char (Fig. 16) is



Oxy-Hb Met-Hb
Salmo alpinus

Fig. 15. A comparison of fresh Oxy-Hb and Hb which had been stored in a refrigerator for several days and changed to Met form. Duration of electrophoresis, 7 hours for Oxy-Hb, 12 hours for Met-Hb.

not thought to give clearly distinctive patterns which might point up any species (or race) difference, and so conclusions as to species or racial differences in these fish are not possible at this time.

The Coregonine fishes studied (Fig. 14) show, depending upon the species, some variance in electrophoretic pattern. *Coregonus nasus* and *Coregonus oxyrhynchus* have very similar patterns and the two leading Hb fractions of both *C. nasus* and *C. oxyrhynchus* separate from the I fraction and are distinct as separate bands after 15—20 minutes of electrophoresis.

The two leading fractions of *Coregonus albula* Hb, however, migrate at very nearly the same speed (Fig. 14) and do not separate into more or less distinct bands until after a long period of electrophoresis. The II and III fractions act very much like samples of Met-Hb (as seen in Vättern char, for example) and are apparent only as an area of greater density in the same band where the two fractions overlap. This may be due to the factors mentioned in the chapter discussing methods.

Because only one species of grayling (*Thymallus thymallus*) is found in Europe (other species or races being found in central and northern Russia etc.), the Hb pattern of this species is comparable only to the Hb of other



Fig. 16. A comparison of Met-Hb from northern and Vättern char. Duration of electrophoresis 8 hour.

Vättern
char northern
 char

salmonid fishes in general. Grayling Hb conforms to the majority of the salmonids in having three Hb fractions (Fig. 1). In the samples examined, the two leading fractions did not separate until they had migrated a long distance together, and then did not become really distinct bands.

Conclusions

During the investigation an attempt was made to obtain as many related species as possible in order to examine the possibility that the Hb of fish might show some family or generic similarity in over-all pattern. Unfortunately the limited number of species available during the survey provides only a provocative hint of some possible family of generic relationships.

The salmonidae have been the largest group investigated by the writer to date, and all indications point to the family having multiple Hb of at least two or three fractions. Of the thirteen salmonid species (or forms) studied or reported by the available literature, nine species show three Hb fractions and four species (or forms) have but two Hb fractions. The interesting point

Table II.

Fish Species	Number of tests	Number of Hb present
<i>CYPRINIDAE</i>		
<i>Leuciscus rutilus</i>	7	1
<i>Leuciscus erythrophthalmus</i>	6	1
<i>Abramis brama</i>	8	2
<i>Abramis blicca</i>	2	2
<i>Phoxinus phoxinus</i>	1 ¹	2
<i>Tinca tinca</i>	3	1
<i>Cyprinus carassius</i>	3	2
<i>Cyprinus auratus</i>	1	1
(<i>Cyprinus carpio</i>)	2 ²	1—2
<i>GADIDAE</i>		
<i>Lota lota</i>	3	2
<i>PERCIDAE</i>		
<i>Perca fluviatilis</i>	8	1
<i>Lucioperca sandra</i>	6	2
<i>Acerina cernua</i>	1	2
<i>ESOCIDAE</i>		
<i>Esox lucius</i> L.	5	2
<i>COTTIDAE</i>		
<i>Cottus poecilopus</i>	1 ¹	2
<i>SALMONIDAE</i>		
<i>Salmo Salar</i>	3	2
<i>Salmo trutta trutta</i>	3	2
<i>Salmo trutta lacustris</i>	3	3
<i>Salmo trutta fario</i> (?)	1 ¹	2
<i>Salmo</i> (<i>Salvelinus</i>) <i>fontinalis</i>	4	3
<i>Salmo</i> (<i>Salvelinus</i>) <i>alpinus</i>	3	3
Lake Vättern char	1	3
<i>Coregonus nasus</i>	9	3
<i>Coregonus oxyrhynchus</i>	2	3
<i>Coregonus albula</i>	3	3
<i>Thymallus thymallus</i>	1	3
(<i>Oncorhynchus keta</i>)	13 ²	2
(<i>Salmo irideus</i>)	5 ^{2 1}	3

¹ Combined blood from a number of individuals.

² Reported by HASHIMOTO and MATSUURA (1959).

here is, that there should be a similarity in the number of obtainable fractions in such widely separated genera as *Salmo* (*salar*) and *Oncorhynchus* (*keta*), while the sub-species (or forms) *Salmo trutta trutta* and *Salmo trutta fario*? have but two fractions and the supposedly closely related subspecies *Salmo trutta lacustris* has three; thus following the trend of the majority of the salmonids studied.

This anomaly may suggest that Hb of species originates independent of genetic (or taxonomic) relationship, in response to some physiological requirement induced by habitat. Hb thus would be a poor indicator of taxonomic relationship. On the other hand, if Hb fractions are inherited under the same genetic laws as govern other blood groups, it seems possible that

Hb proteins may be used in taxonomic studies with some degree of accuracy. The seeming anomaly of the *Salmo trutta* subspecies (or forms) would then be in reality a reflection of real differences. An other alternative is, of course, that electrophoresis or the treatment given samples creates artificial similarities or dissimilarities as the case may be. It will be necessary in future work to include other methods of analysis such as heat coagulation, spectrophotometry etc. to confirm the electrophoretic findings.

The species investigated to date, with few exceptions (i.e. the brown trout forms), seem to indicate that Hb is a good indicator of genetic relationship because many species studied show strong generic or family similarities. No instance was noted where one species had a different number of Hb fractions than other species of the same genus (Table II), although each species, with few exceptions, seems to have Hb components which migrate with distinctive velocities. Of twenty-three species only two or possibly four species (*Leuciscus rutilus* and *L. erythrophthalmus* being distinctive in this connection) have Hb fractions which migrate with identical velocities. Further work, particularly with attention to isoelectric points, with these species might result in the possibility of demonstrating differences in their Hb. This is almost certain in the case of the *Coregonus* species mentioned where three Hb fractions are involved.

In general, this study has not resulted in enough concrete evidence to allow definite taxonomic comparisons to be made. The many variable factors which have entered into the work allow only relative comparisons to be made, but these often show very great differences between the species Hb. The study in fact has but formed the ground work for a much more intensive study in species Hb relationships to be attempted in future work. A problem none the less interesting concerns the function of the various Hb fractions in the physiological processes of the various species.

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